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Growth index inheritance, selection and trait associations in pearl millet

Peter James Lynch
Iowa State University

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**Growth index inheritance, selection, and trait associations in
pearl millet**

Lynch, Peter James, Ph.D.

Iowa State University, 1993

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

**Growth index inheritance, selection and,
trait associations in pearl millet**

by


Peter James Lynch

**A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
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**Iowa State University
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1993**

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GENERAL INTRODUCTION

Growth rate is the increase in dry weight of plants per unit of land per unit of time, e.g., $\text{g m}^{-2} \text{ day}^{-1}$. Typically, it is measured at several times during the season, via daily or weekly harvests of plants from equal-size land areas. Growth rate is laborious to measure and generally estimated for only a few genotypes. However, growth index (GI), an estimate of vegetative growth rate obtained from one or two harvests during the season, has been described for oat, Avena sativa L. (Takeda and Frey, 1976; Gupta et al., 1987) and pearl millet, Pennisetum glaucum (L.) R. Br. (Bramel-Cox et al., 1984). That vegetative growth rate can be estimated via GI for a large number of oat or pearl millet genotypes makes its selection practical in a breeding program.

GI is related to grain yield for cereals by the formula: Grain yield = GI x growth duration x harvest index (Takeda and Frey, 1977). GI x growth duration equals biomass, and harvest index represents how much of biomass is partitioned to grain. For oat grown in the midwest U.S.A., growth duration is short and harvest index has been optimized at ca. 45% (Rosielle and Frey, 1975; Takeda and Frey, 1977), leaving selection of GI as the most likely method for increasing grain yield of oat. As with oat grown in the midwest U.S.A., the growth duration for pearl millet grown in India is short, 70 - 100 days (Virmani et al., 1982). Thus, GI may be a useful strategy for improving grain yield in pearl millet.

Genetic variation for growth rate is limited in the cultivated oat (Lynch and Frey, 1993; Cox and Frey, 1984), barley, Hordeum vulgare L. (Riggs et al., 1981), and pearl millet gene pools (Bramel-Cox et al., 1984). Thus, increasing GI may be difficult. However, in oat and pearl millet, matings between cultivated and wild and weedy relatives have resulted in increased genetic variation for GI (Cox and Frey, 1984; Bramel-Cox, 1986).

Because the minimum information necessary to select for GI in pearl millet is available, that is, a method to estimate GI and sources of genes for high GI, the general objective of this dissertation research was to further investigate selection for GI as a method of improving breeding populations of pearl millet.

My specific objectives were to:

1. Determine the inheritance of GI measured at 10 d after bloom date (i.e., GI1) and at maturity (i.e., GI2) and several traits related to GI from matings among two elite varieties and three landraces of pearl millet;
2. Evaluate the response from one cycle of S_1 -line recurrent selection for increased GI1 in the Higrop and Senpop pearl millet gene pools;
3. Determine the correlated responses among unselected traits from selection for GI1 in Higrop and Senpop; and

4. Determine the phenotypic and genotypic correlations of GI1 and grain yield with other agronomic traits in Higrop and Senpop.

Explanation of Dissertation Format

This dissertation contains three papers. In paper I genetic effects for GI, and six traits related to GI from matings among two elite varieties and three Indian and African landraces of pearl millet are presented. In paper II the direct response from one cycle of S_1 -line recurrent selection for GI in the Higrop and Senpop genepools are presented. The indirect responses from selection for GI in Higrop and Senpop among eleven unselected traits and the phenotypic and genotypic correlation of vegetative growth rate with the unselected traits are presented in paper III.

Each paper was written as a manuscript for publication in a journal. The General Introduction and the Literature Review precede the first paper, and the General Conclusions and Discussion follow paper III. References in the General Introduction, Literature Review, and General Conclusions and Discussions are listed in the Additional References section. Supplemental information for the three papers that is not intended for publication is presented in the Appendix.

LITERATURE REVIEW

Growth Rate

Growth rate is estimated for some interval of time by cutting all plants from a unit of land and measuring their dry-weight on the first and last date of the interval. The interval is some portion of the vegetative phase, reproductive phase, or for the entire growing season, and estimates of vegetative, reproductive and whole-season growth rates, respectively, result. Growth rate can be expressed in absolute terms, i.e., $\text{g m}^{-1} \text{d}^{-1}$, or in relative terms, i.e., $\text{g g}^{-1} \text{m}^{-2} \text{d}^{-1}$ (Radford, 1967). It has been used to quantify the effects of plant breeding (Riggs, 1981; Karimi and Siddique, 1991; Lynch and Frey, 1993), and to compare ancient forms (Gardner et al., 1990) and wild species (Bramel-Cox, 1985) with their modern cultivated relatives. Estimation of growth rate via a standard growth analysis is arduous. For this reason, it has not been used widely as a trait for selection by plant breeders.

Growth rate of oat

The most thorough investigation of GI as a trait for selection in a crop species has been conducted in oat. Research on GI in oat originated from an observation made during the development of the E (early) and M (midseason) series of multiline oat cultivars (Frey et al., 1971a,b). The near-isogenic lines used as components in the multiline cultivars were developed by back-crossing crown rust (Puccinia coronata Cda. avenae Frazier and Led.) resistance genes from several

donors, including accessions of Avena sterilis, into an early or midseason recurrent parent. When one of these crown rust resistance genes, from CI 8079, was placed in near-isogenic lines and compared in disease-free environment, grain yields were from 5% to 7% greater than the recurrent parents (Frey and Browning, 1971). Lawrence and Frey (1975) observed BC₂ and BC₄ segregates from A. sativa x A. sterilis matings that produced grain yields 27% to 30% greater than their recurrent parent. Other agronomic traits of the higher yielding near-isogenic lines were similar to the recurrent parents. In subsequent studies it was found that:

1) The greater grain yields of backcross derived lines from A. sativa and A. sterilis matings were associated with: a) greater leaf area and leaf area duration (Bleothe-Helsel and Frey, 1978; Brinkman and Frey, 1977a); and b) increased numbers of spikelets per panicle, increased panicle number, and increased seed weight (Brinkman and Frey, 1977b).

2) Harvest index and GI accounted for 92% of the variation for grain yield among 1200 lines derived from A. sativa and A. sterilis matings (Takeda and Frey, 1976).

3) GI for oat a) is quantitatively inherited; b) has moderately high heritability (0.40); c) is weakly associated with or independent of heading date, plant height, and harvest index; d) possesses strong genetic correlations with grain yield (0.59 - 0.87); and e) likely could

be combined with agronomically acceptable breeding lines to produce oat lines with high grain yield (Takeda and Frey, 1977).

4) GI could be measured as straw weight divided by days to heading (Gupta et al., 1987).

5) Treatment of seeds with ethidium bromide did not produced useful mutations for GI (Jalani and Frey, 1979).

6) In the cultivated oat gene pool, transgressive segregates for increased GI were more frequent from adapted x exotic than from adapted x adapted cultivar matings (Takeda et al., 1979).

7) The frequency of plus-transgressive segregates for GI and biomass was greater from inter-specific than from intra-specific matings (Cox and Frey, 1984).

Growth rate of pearl millet

Begg (1965) reported growth rates of $44 \text{ g m}^{-2} \text{ d}^{-1}$ during the ninth week of development for a pearl millet forage cultivar. Pearson et al. (1977) found that pearl millet had greater growth rate during the three weeks following emergence than did maize (Zea mays L.) or hybrid Pennisitum, but the highest growth rate recorded, more than twice that of pearl millet, was for a maize hybrid.

Despite recent studies on the growth and development of pearl millet when used as a grain and fodder crop in the Semi-Arid Tropics (e.g., Gregory and Squire, 1979; Ong 1983a,b; Carberry et al., 1985; Batanio et al., 1990), few estimates of growth rate for pearl millet as

a cereal crop when grown in this region have been reported. However, when straw or plant weight and days to flowering or maturity are reported, either a vegetative or whole-season growth rate can be computed. For example, Craufurd and Bidinger (1988) reported whole season growth rate (plant weight/days to maturity) for two pearl millet hybrids were 13.14 and 12.88 g m² d⁻¹ with daylengths of 12.5 h d⁻¹ and 19.45 and 17.39 g m² d⁻¹ for a daylength of 15.5 h d⁻¹. Because the grain weight for a hybrid was not different between the two daylength treatments, the vegetative growth rate of a hybrid increased when the daylength was increased.

Ong and Monteith (1985) concluded that light determines the growth rate of pearl millet at any stage of development; however, development can be reduced by low light intensity and growth can be impaired by high or low temperature. Soil moisture (Kassam and Kowal, 1975; Azam-Ali et al., 1984) and soil fertility (Coaldrake and Pearson, 1985; Payne et al., 1991) also influence growth rate of pearl millet.

Bramel-Cox et al. (1984) studied the growth on each of four hybrid and landrace varieties, three weedy (ssp. stenostachyum) and one wild (ssp. monodii) subspecies of pearl millet from India and Africa and found that vegetative growth rate, that is growth index, could be estimated either at 10 days after flowering or at maturity by the formula: (Vegetative dry weight at flowering + 10 days, or at maturity)/(number of days to flowering + 10). The wild subspecies had a GI that was significantly greater than those of other entries. Using

this formula, Bramel-Cox et al., 1986) evaluated a wild (*ssp. monodii*) and a weedy (*ssp. stenostachyum*) subspecies accession and a primitive landrace accession of pearl millet when crossed with two adapted pearl millet inbred lines for improving GI and grain yield of pearl millet. They identified lines with increased GI and grain yield from all matings, although the wild accession was the best source of genes for improving GI, whereas the primitive landrace and the weedy relative were the best sources for improving grain yield. No strong associations existed among 17 traits measured on the lines that would impede recombination of cultivated and exotic parent genes (Bramel-Cox et al., 1987).

Selection for Physiological Grain Yield Components

Anatomical components of grain yield typically suggested for cereal crops are number of culms per plant, number of seeds per inflorescence, and weight per seed. Physiological processes have been suggested as components of grain yield as well. For example, in dry environments, grain yield as the product of available water, water use efficiency of available water (g of above ground biomass per g of water), and harvest index has been proposed for wheat, *Triticum aestivum* L. (Passioura, 1977) and for sorghum (*Sorghum bicolor* L.) and chickpea, *Cicer arietinum* L. (Ludlow and Muchow, 1988). Takeda and Frey (1976) suggested that grain yield for cereals with a short growth duration is the product of growth rate, growth duration, and harvest index.

Grain yield is determined by the rate at which assimilates are translocated into the grain, and the duration of assimilate translocation. Selection for increased rate and duration of grain filling have been proposed as methods for increasing grain yield for maize (Ponneleit et al., 1980;). Hartung et al. (1989) found that three cycles of phenotypic recurrent selection for increased rate of maize grain filling gave a 13% grain yield increase, but selection for increased duration of grain filling caused no change in the grain yield.

Nitrate reductase reduces nitrate to nitrite, and often is the rate-limiting step of nitrate assimilation by plants. Eichelberger et al. (1989) found that eight cycles of divergent selection for nitrate reductase activity (NRA) in maize increased and decreased post-anthesis leaf lamina NRA by 46% and 62%, respectively. However, by C₆ selection for increased and decreased post-anthesis leaf lamina NRA caused grain yield to decrease by 5.6% and 16.8%, respectively.

Recurrent Selection in Pearl Millet

Recurrent selection has been used for improving allogamous crops (Hallauer, 1985), and autogamous crops (Frey et al., 1988). However, few published results exist in which recurrent selection was utilized to improve pearl millet when it is grown as a cereal crop. The tremendous genetic variation, allogamous breeding behavior, protogynous floral structure, and ease of producing various types of progenies, make pearl millet amenable to recurrent selection (Rachie and Majmudar, 1980).

Mass selection in pearl millet has increased forage yield per plant, stem thickness, and tiller number (Gupta and Choubey, 1984), and grain yield per plant (Rattunde et al., 1989). Two cycles of reciprocal and full-sib recurrent selection in the Delhi composite increased grain per plant by 21% and 17%, respectively (Govil, et al., 1982), while two cycles of S_1 recurrent selection in the World, Nigerian, and Ex-Borno pearl millet composites increased grain yield by 12%, 10%, and 10%, respectively (Khadr, 1977). When averaged over two populations, two cycles of half- and full-sib recurrent selection for tolerance to high temperature during emergence increased the emergence of seedlings grown at 45° C by 14.8% (Lynch, 1993).

PAPER I. THE INHERITANCE OF VEGETATIVE GROWTH INDEX
AND RELATED TRAITS IN PEARL MILLET PENNISITUM
GLAUCUM (L.) R. Br.

ABSTRACT

To provide pearl millet breeders with information for devising the most efficient breeding method to improve growth index (GI) in pearl millet, a generation means analysis was conducted to determine the significance and relative importance of four genetic parameters, namely additive, dominance, heterotic, and additive x additive epistatic genetic effects, that could be operational in the inheritance of GI in pearl millet. Two elite and three landrace varieties of pearl millet were mated, and the parents, parents selfed, the F_1 s, F_1 s selfed, and F_1 s random mated were evaluated in 1990 and 1991 at the International Crops Research Institute for the Semi-Arid Tropic, near Hyderabad, India. Traits measured were GI at 10 days after bloom date (GI1) and at maturity (GI2), bloom date, straw yield, biomass, harvest index, and plant height. The fully fitted genetic model explained from 88% to 95% of the variation among the generations for the measured traits. Additive effects accounted for the largest proportion of the generations sums of squares for all the traits except GI2, straw yield, and biomass, for which additive x additive epistatic effects were of greatest importance. Although inheritance patterns for GI1 and GI2 were dissimilar, any breeding method that selects for additive effects should be suitable for improving them. However, if GI2 is selected, maximum improvement will occur only if the breeding method also selects for dominance genetic effects.

INTRODUCTION

Selection for increased growth rate (GI) was proposed by Takeda and Frey (1977) as a means for increasing grain yield of cereals with a short growth duration. In India, pearl millet (Pennisetum glaucum (L.) R. Br.] is a short-duration crop grown for its grain and fodder, and its productivity may benefit from selection for increased GI. Bramel-Cox et al. (1984) devised a rapid method for estimating GI for pearl millet, and were able to select lines with significantly greater GI.

The breeding method that will be most efficient for improving a trait is determined largely by the trait's inheritance. Growth index of pearl millet appears to be quantitatively inherited (Rattunde et al., 1989; Bramel-Cox et al., 1986). However, the inheritance of GI of pearl millet has not been studied. The objective of this study was to determine the significance and relative importance of four genetic parameters that could be operational in the inheritance of GI when measured at 10 days after bloom date (i.e., GI1) and at maturity (i.e., GI2) and of five traits related to growth rate.

MATERIALS AND METHODS

Development of Genetic Materials

The five populations of pearl millet used to initiate this study were: (a) ECC6, a variety from the sixth cycle of selection for grain yield and earliness in the Early Composite carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT); (b) VC F₂, the self pollinated progeny from mating ICMV 87901 and ICMV 82132; and (c) IP 3226, IP 3175, and IP 6098, ICRISAT landrace accessions collected in western and central Rajasthan state in India, and in Niger, respectively. These parents are typical of germplasm used for breeding populations at ICRISAT. Matings among the five parents were made at ICRISAT during the November - January season, 1989-90, via a diallel mating plan, without reciprocals. Matings were produced via full-sibing at least 100 plants per parent per mating, except for IP 3226 x IP 6098, IP 3175 x IP 6098, and VC F₂ x IP 6098, in which 97, 68, and 50 plants, respectively, per mating were used. At maturity, each full-sib progeny within a mating was cut, sun-dried, and threshed separately. A bulk seed lot was made by compositing 10-ml samples of seed from all full-sib progenies within a mating. The composites represented population matings.

During the March - May season, 1990, the F₁ population matings were remade and the population-mating composites that were produced in the November - January season, 1989-90 were selfed and random mated. Also, the parent populations were random mated and selfed. The random

mated generations were produced via a series of full-sib progenies. At least 150 plants were used for producing either self pollinated or full-sib progenies of a generation. At maturity each selfed or full-sib progeny within a mating was harvested, sun-dried, and threshed separately. Next, 10-ml samples of seed from all panicles selfed or full-sibed within a mating were composited. These composites were the source of seed used for the evaluation experiments. Thus, seed lots of all generations of all matings were produced in the same season and field.

Field Evaluations

Evaluation experiments were conducted during the June - October season 1990 and 1991 at ICRISAT. Each experiment contained (a) 40 experimental entries representing the five parents random mated, the five parents selfed, the F_1 s of the 10 matings, the F_1 s of the 10 matings random mated, and the F_1 s of the 10 matings selfed, and eight (1990) or nine (1991) checks. The checks were: ICMV 87901, ICMV 82132, ICMV 84400 (in 1991 only), and WCC75, high yielding varieties developed at ICRISAT; HHB67, a very early maturity hybrid; ICMH 423 and ICMH 501, early and medium maturity ICRISAT hybrids, respectively; and Higrop C_0 and Senpop C_1 , gene pools formed by intermating landrace accessions and wild and weedy subspecies (*ssp. monodii* and *stenostachyum*) relatives, all of which had high GI1, with improved pearl millet varieties (Bramel-Cox et al., 1984).

Each experiment contained three replications. A plot was four 4-m rows, and rows were spaced 75 cm apart. Planting dates were 25 June in 1990 and 14 July in 1991. At ca. 14 days after emergence, seedlings were thinned to one plant per 15 cm of row. Each experiment received a pre-plant broadcast application of 40 and 17 kg ha⁻¹ of nitrogen and phosphorus, respectively, and a side-dressing of 40 kg ha⁻¹ of N applied as urea at 20 days post emergence. Plots were hand-weeded. Grain harvest occurred when seeds on the main panicle were at the black-layer stage (Fussel and Pearson, 1978). In 1991, the experiment was irrigated at 14 and 50 days after sowing. Traits measured on each plot are presented in Table 1.

Table 1. Traits measured or computed.

Trait	Abbreviation	Calculation	Units
<u>Traits analyzed</u>			
Bloom date	BD		d
Growth Index at BD + 10 days	GI1	(SW1/PSZ1)/(BD + 10)	g m ⁻² d ⁻¹
Growth Index at maturity	GI2	(SW2/PSZ2)/(BD + 10)	g m ⁻² d ⁻¹
Biomass	BM	PW + SW2	g m ⁻²
Harvest index	HI	GW/BM	%
Plant height	PH		cm
Straw yield	SY	SW2/PSZ2	g m ⁻²
<u>Traits measured for computations</u>			
Plant count	PC		# plot ⁻¹
Plot size for GI1	PSZ1		m ²
Plot size for GI2	PSZ2		m ²
Straw weight at BD+10	SW1		g plot ⁻¹
Straw weight at maturity	SW2		g plot ⁻¹
Grain weight	GW		g m ²

Statistical Analysis

All analyses were performed using PROC GLM of PC-SAS (SAS, 1987). Analyses of variance were performed on the data from individual years and then combined. Another analysis was conducted upon the means of the population generations in each year and across years when combined by using a model of Gardner and Eberhart (1966). In this model each generation mean for a trait (Y) is written as a function of the cumulative additive (a), dominance (d), heterotic (h) and additive x additive epistatic (aa) genetic effects. The coefficients of these parameters change depending upon the generation used. For example the model for the mean of the i^{th} parent is $Y_i = \mu + a_i + d_i$, where Y_i is the mean of parent i , μ is the mean of all generations, a_i is the cumulative additive effects for parent i , and the model for the F_1 of the $i \times j$ mating is $Y_{ij} = \mu + 0.5(a_i + a_j) + 0.5(d_i + d_j) + h_{ij} + aa_{ij}$, where Y_{ij} is the generation mean of i^{th} and j^{th} parent, μ is the mean effect of all populations, a_i and a_j are the cumulative additive genetic effects for parents i and j , respectively, d_i and d_j are the cumulative dominance genetic effects parents i and j , h_{ij} is the heterotic effect of from the $i \times j$ mating, and aa_{ij} is the additive x additive epistatic effects from the $i \times j$ mating. The genetic parameters that contribute significantly to a trait and the sums of squares associated with each genetic parameter are determined by successively fitting more complex models to the data via least squares regression. The means squares due to fitting each genetic parameter are 1) tested for significance and 2) compared

with the generations sum of squares for a trait. The generations sum of squares not accounted for by the fully fitted genetic model are termed residual, and it represents effects involving dominance epistasis and linkage.

F-tests were used to determine significance of mean squares due to differences among main effects, interactions, and genetic parameters by using the entry x year mean square. When the entry x year effect was non-significant, this source of variation was pooled with the error mean square. The degrees of freedom associated with this pooled error were the sum of degrees of freedom for error and entry x year interaction. This pooled error was then used to make all tests of significance. Missing values were generated by the LSMEANS procedure in SAS (SAS, 1987). One degree of freedom was subtracted from the error term for each missing value.

RESULTS AND DISCUSSION

Significant differences occurred among generations for all seven traits (Table 2). Additive genetic effects were significant for all traits, except GI2, dominance effects were significant for all traits but GI1, heterotic effects were significant for all traits except GI1 and GI2, and additive x additive epistasis effects were significant for all traits except GI1. Residual effects, which in this model can be due to linkage effects or epistasis involving dominance, were significant for BD, HI and PH.

The inheritance patterns for GI1 and GI2 were different. For GI1, only additive genetic effects were significant whereas for GI2, dominance and additive x additive epistatic genetic effects were significant. Previously, Bramel-Cox et al. (1984) showed that accumulation of vegetative dry weight in pearl millet ceased at 10 days after 50% of the main-stem panicles had emerged stigmas (i.e., BD). Thus, growth rate estimated either at BD+10 (i.e., GI1) or maturity (i.e., GI2) should be determined by similar genetic effects. Therefore, different inheritance patterns for GI1 and GI2 were not expected.

To better understand the different inheritance patterns for GI1 and GI2, means for the F_1 , F_1 selfed, and the F_1 random mated generations for GI1 and GI2 were compared (Table 3). Means for GI1 and GI2 were similar for the F_1 and for the F_1 selfed generations, indicating that in these generations vegetative growth rate did not change during the interval BD+10 days to maturity. This corroborates

Table 2. Means square for generations, four genetic parameters, and residual effects of generation means for several traits of pearl millet evaluated in 1990 and 1991 and analyzed by using Eberhart-Gardner (1966) model.

Source of variation	Traits							
	df	BD	GI1	GI2	SY	BM	HI	PH
Generations	39	132.6**	5.8**	8.7**	27183.6**	93994.2**	179.0**	2502.2*
Additive	4	394.2**	21.0**	4.0	21148.9**	161063.2**	798.6**	10779.8**
Dominance	5	69.3**	5.9	19.9**	35540.4**	214132.0**	98.9**	771.2**
Heterotic	10	137.7**	3.1	3.7	22351.0**	45471.8*	207.5**	1817.0**
Additive x additive epistatic	10	142.3**	5.7	14.7**	49491.9**	133532.4**	80.5**	2464.4**
Residual	10	44.7**	2.6	3.9	7943.1	16081.8	41.4**	779.8**

*,**Indicates significance at 0.05 and 0.01 levels, respectively.

Table 3. Means for growth index estimated ten days after flowering (GI1) and at maturity (GI2) for the F_1 , F_1 selfed, and F_1 random mated generations of pearl millet.

Generation	GI1	GI2
	<hr/> g m ² d ⁻¹ <hr/>	
F_1	6.36	6.39
F_1 selfed	5.54	5.64
F_1 random mated	5.20	4.50

the results of Bramel-Cox et al. (1984), namely, that, growth rate can be satisfactorily measured either at 10 d after flowering or at maturity. However, the means for the F_1 selfed and the F_1 random mated generations for GI1 differed by 0.34 g m² day⁻¹, whereas for GI2 they differed by 1.14 g m² day⁻¹. This larger difference between the F_1 selfed and the F_1 random mated for GI2 likely is the cause of the difference in inheritance pattern for GI1 and GI2. An explanation is provided by the mean expectations for the F_1 self pollinated and F_1 random mated generations, which respectively are:

$$Y_{12}^s = \mu + 0.5(a_1 + aa_1 + a_2 + aa_2) + 0.25(d_1 + d_2) + 0.5(h_{12}) + aa_{12}$$

$$Y_{12}^r = \mu + 0.5(a_1 + aa_1 + a_2 + aa_2) + 0.5(d_1 + d_2) + 0.5(h_{12}) + aa_{12}.$$

Based upon these expectations, the significant dominance genetic effects for GI2 arise from the greater coefficient for the "d" effect in the F_1 random mated (0.5) versus the F_1 selfed (0.25), whereas the significant additive x additive epistatic effects arise from the larger difference between the F_1 selfed and the F_1 random mated generations for GI2 than occurred for GI1. Presumably, random mating broke favorable epistatic

linkages, and this effect was greater for GI2 than GI1. However, this should not change the breeding method used to improve growth rate when it is estimated either at BD+10 or at maturity.

The proportion of the generations sums of squares accounted for by this genetic model ranged from 88% for GI2, to 95% for BM (Table 4), indicating that the model explained variation among the generation means adequately. Of the four genetic parameters estimated, additive effects accounted for the largest proportion of the generations sums of squares for all the traits except GI2, SY, and BM; for these traits additive x additive epistatic effects were of greatest importance. In fact, for all seven traits, a greater proportion of the generation sums of squares were accounted for by the sum of additive effects and additive x additive epistatic effects (48% to 69% of the generations sums of squares) than by the sum of dominance and heterotic genetic effects (23% to 41% of the generations sums of squares). For GI1 and GI2, additive plus additive x additive epistatic effects accounted for 67% and 48% of the generations sums of squares, respectively, whereas dominance and heterotic effects accounted for 23% and 40% of the generations sums of squares for GI1 and GI2, respectively.

Studies of inheritance of vegetative growth rate in crop species are confined to oat (Avena sativa L.). Helsel and Frey (1983) found that among 12 A. sterilis x A. sativa matings inheritance of vegetative

Table 4. Percentages of generations effect sums of squares due to the variance of the genetic parameters.

Genetic effect	Traits						
	BD	GI1	GI2	SY	BM	HI	PH
Additive (a)	30	39	5	5	18	46	44
Dominance (d)	7	7	29	29	29	7	4
Heterotic (h)	27	16	11	11	12	30	19
Additive x additive epistatic (aa)	28	28	43	44	36	12	25
Residual	9	10	12	11	5	5	8

growth rate was additive for seven matings and non-additive for five. Results from this study tend to agree with those of Helsel and Frey (1983), i.e., additive effects probably are of greatest importance in the inheritance of growth rate but dominance effects should not be ignored. Takeda et al. (1979) reported that the minimum number of effective factor pairs segregating for vegetative growth rate ranged from 6 to 9 for 23 matings among adapted x adapted, adapted x exotic, and adapted x semi-exotic oat cultivars and lines. For populations from matings of A. sativa x A. sterilis, Takeda and Frey (1977) estimated minimum number of effective factor pairs segregating for vegetative growth rate ranged from 3 to 9. Burton (1959) reported that among 818 single cross hybrids of pearl millet, 55.9% of the genetic variation for forage yield was non-additive. Later, Burton (1968a) demonstrated that this was largely due to dominance genetic variance, even though

epistasis was important in some crosses (Burton, 1968b). In my study, SY and BM are the traits most closely related to forage yield, and for these traits the dominance and heterotic effects accounted for 40% of the variation in generations sums of squares.

This study used only five parents: Therefore, extrapolating results from it to all pearl millet germplasm is not justified. The varied inheritance patterns among matings of oat confirm that inheritance for vegetative growth rate can differ among crosses. Despite the small number of parents I used, they comprise both elite cultivated and exotic sources of pearl millet germplasm. They are representative of germplasm that likely would be used in an intensive selection program to improve vegetative growth rate. In fact, exotic pearl millet germplasm can be an excellent source of genes for increased GI (Bramel-Cox et al., 1984).

Despite a difference in inheritance patterns for GI1 and GI2, this study shows that additive and additive x additive epistatic genetic effects are of major importance in the determination of either GI1 or GI2. Any breeding method that selects for additive effects should be suitable for improvement of vegetative growth rate. However, if GI2 is selected, maximum improvement will be realized only if the breeding method used to improve growth rate also selects upon dominance types of genetic effects.

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PAPER II. RECURRENT SELECTION FOR VEGETATIVE GROWTH INDEX
IN PEARL MILLET (PENNISETUM GLAUCUM (L.) R. Br.)

ABSTRACT

The Higrop and Senpop gene pools were formed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to assess the efficacy of selection for vegetative growth index (GI) for improving grain yield in pearl millet. In 1991, C₀ and C₁ cycle populations and 46 random S₁ lines from C₀ and C₁ of Higrop and Senpop and were evaluated in India for bloom date (BD), grain yield (GY), and GI at 10 d after flowering (GI₁). Selection in Senpop decreased BD (4.8 d) and increased GI₁ (3.2 g m⁻² d⁻¹) when cycle populations were grown. In Higrop, cycle population means were not significantly different, although BD decreased (4%) and GY increased (5%). When S₁ lines were evaluated, progress occurred for all traits: In Higrop, BD decreased (4.7%), GY significantly increased (17.9 g m⁻²), and GI₁ increased (7.1%) and in Senpop, BD decreased (7.7%), GY increased (16.9%), and GI₁ increased (4.6%). Heritabilities in Higrop and Senpop were high for BD (i.e., 0.90) and moderate for GY and GI₁ (i.e., 0.45). Simultaneous improvement in BD, GY, and GI₁ was attributed to the selection procedure employed, which included culling of high GI₁ with late maturity and/or low grain yield. Subsequent cycles of selection for increased GI₁ in Higrop and Senpop should be successful.

INTRODUCTION

Typically, the components of grain yield are considered to be number of culms per plant, numbers of seeds per inflorescence, and weight per seed. Takeda and Frey (1977) suggested an alternate partition for grain yield of cereals as: Grain yield = growth index x growth duration x harvest index. The product of growth index (GI) and growth duration is biomass, and harvest index is the ratio of grain weight to biomass. For oat (Avena sativa L.) grown in central U.S.A., growth duration cannot be extended because unfavorable growing conditions occur late in the growing season, and harvest index is at or near optimum. Thus, Takeda and Frey (1977) suggested that GI was the best trait to select for increasing grain yield of this crop.

As with oat grown in the Midwest USA, the growth duration for pearl millet [Pennisetum glaucum (L.) R. Br.] grown in India is short, generally from 70 - 100 days after planting (Virmani et al., 1982). Thus, selection for increased GI may result in greater grain yield for pearl millet. However, for GI to be selected in breeding program, a rapid and inexpensive method for its estimation is required. Bramel-Cox et al. (1984) determined that the GI for pearl millet can be estimated either at 10 days after bloom date (GI1) or at maturity (GI2) by the formula: (vegetative dry weight at days to bloom + 10 days, or at maturity)/(number of days to bloom + 10). Using this method for estimating GI, Bramel-Cox et al. (1986) identified genetic variation for GI1 and transgressive segregates with increased GI1.

In this study, I evaluated the response from one cycle of selection for increased GI1 in Higrop and Senpop, pearl millet gene pools, formed by intermating high GI1 progenies derived from matings between an elite pearl millet population and accessions of landrace, weedy (ssp. stenostachyum), and wild (ssp. monodii) pearl millet.

MATERIALS AND METHODS

Gene Pool Development

The plant populations used for this study were Higrop (High Growth Rate Population) and Senpop (Senegal Population), gene pools formed at The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, to evaluate the potential of exotic germplasm for increasing GI1 of cultivated pearl millet (Bramel-Cox et al., 1986).

The formation of Higrop and Senpop began in the March - May season, 1988 when four landraces, two wild subspecies [*ssp. monodii* (Maire) Brunken], and two weedy subspecies [*ssp. stenostachyum* (Klotzsch ex A. Br. and Bouche) Brunken] of pearl millet, collected in India and Africa, were crossed onto an F_2 population. The F_2 was from the mating ICMV 87901 x ICMV 82132. The ICMV parents were ICRISAT varieties with medium maturity and high grain yield. In the November - February season, 1988-89, the F_1 s from wild and weedy *ssp.* matings were backcrossed to the F_2 and the F_1 s involving the landraces were random mated. In the March - May season, 1989 the seeds from the random matings and $BC_1 F_1$ s were space-planted and selfed to form S_1 lines and $BC_1 F_2$ lines. In the July - October season, 1989, 38 S_1 or $BC_1 F_2$ lines from each landrace mating and each wild and weedy *ssp.* BC_1 mating, along with 20 checks, were evaluated in an 18 x 18 lattice experiment with two replications in a field at ICRISAT Center. The 20 S_1 or $BC_1 F_2$ lines from this trial that had the highest GI1 (Bramel-Cox et al., 1984) and acceptable grain

yields and maturities were intermated to initiate the Higrop gene pool. Next, a BC_1 mating which involved a weedy accession from Senegal was judged to be the best of the eight matings on the basis of the means of its 38 $BC_1 F_2$ lines for G11, grain yield, and maturity. The 20 $BC_1 F_2$ lines from this mating with the highest G11's were intermated to initiate the Senpop gene pool.

To intermate the 20 S_1 and $BC_1 F_2$ lines selected to initiate Higrop, a bulk of pollen from n plants in each of the 20 lines was used to pollinate n plants in each of the 20 lines. This intermating plan was continued daily until ca. 25 plants had been pollinated in each of the 20 selected lines. A plant was used only once as a male or female. Seeds from a crossed panicle was a half-sib family. $BC_1 F_2$ lines selected to form Senpop were intermated via a diallel mating plan in which the pollen from one plant within a line was used to pollinate one plant in a different line. The crossing was continued until one plant within each $BC_1 F_2$ line had been crossed with one plant in each of the remaining 19 $BC_1 F_2$ lines. A plant was used only once as a male or female. This crossing procedure was executed twice to produce 380 full-sib progenies.

At maturity, the crossed panicles were cut, sun-dried, and threshed individually. The C_0 populations were formed by bulking ca. 10 g of seed from (a) each of the ca. 500 half-sib progenies in Higrop and (b) each of the ca. 380 full-sib progenies in Senpop.

Recurrent Selection Procedure

The single cycle of recurrent selection conducted in Higrop and Senpop, consisted of three phases: (1) Field evaluation of random S_1 lines, (2) recombination of the 20 S_1 lines that had high GI1 and acceptable grain yields and numbers of days to flowering, and (3) production of random S_1 lines.

In July - October 1990 134 random S_1 progenies from the C_0 of each gene pool plus 10 check entries were evaluated in a 12 x 12 lattice design at two locations in India. Planting dates were on 25 June at ICRISAT Center and 9 July at Hisar, Harayana. A plot was two 4-m rows spaced 75 cm apart. At ca. 14 days after emergence, seedlings were thinned to approximately one plant per 10 cm of row. Each experiment received a pre-plant broadcast application of 40 and 17 kg ha⁻¹ of nitrogen and phosphorus, respectively. Side-dressings of ca. 40 and 20 kg ha⁻¹ of N (as urea) were applied 20 days after emergence was performed at ICRISAT Center and Hisar, respectively. Plots were hand-weeded twice.

During November - March 1990-91 the 20 S_1 lines with high GI1 and acceptable grain yields and bloom dates from each gene pool were intermated. As described for making the C_0 populations, half-sib matings were made for recombining the selected lines in Higrop and full-sib matings were made for recombining the selected lines in Senpop. At maturity (Fussel and Pearson, 1978) all crossed panicles within a gene pool were harvested, threshed individually, and ca. 10-g seed lots from

all progenies were bulked to produce the C1 population. Also in this season, the 20 S₁ lines with highest GI1 from each gene pool (i.e., no consideration was given to grain yield or bloom date) were recombined and designated SGI1 C1, for single-trait GI1 selection.

In February - May 1991 ca. 300 plants from C0 and C1 populations of each gene pool were grown at wide spacing (50 cm between plants), and all panicles on a plant were selfed. At maturity, all selfed heads of a plant were harvested, dried, and threshed. This bulk of seed from an S₀ plant represented an S₁ line.

Evaluation of Progress From Selection

Two experiments were conducted during the July - October, 1991 to evaluate progress from selection for increased GI1. The first experiment (Experiment 1) contained 49 entries: (a) C0 and C1 of Higrop and Senpop, (b) Single-trait GI1 selection (SGI1) C1 from both gene pools, (c) the 8 F₂ populations from the matings of ICMV 87901 x ICMV 82132 with the four landrace, two weedy ssp., and two wild ssp. accessions repeated twice, (d) seven open pollinated checks, and (d) seven F₁ hybrid check varieties, (e) ten populations from a selection study designed to increase tolerance in pearl millet to high temperature during germination and emergence and three check entries related to that study. The entries were evaluated in four replications of a randomized complete block experiment, at each of three sites in India: Bhavanisagar (11°N), ICRISAT Center (17°N), and Hisar (29°N). Planting

dates were 27 June at Bhavanisagar, 14 July at ICRISAT Center, and 4 July at Hisar. A plot consisted of four 4-m rows, with rows spaced 75 cm apart at ICRISAT Center and Hisar, and 50 cm apart at Bhavanisagar. Seedlings were thinned to ca. 10 cm intervals at all sites. The experiment at ICRISAT Center was irrigated twice after flowering occurred, whereas at Bhavanisagar and Hisar the experiments were irrigated throughout the season. The experiment at Bhavanisagar received 20 kg N, 26 Kg P, and 37 kg K ha⁻¹ before planting and topdressings of ca. 20 kg N ha⁻¹ at 15 and 30 days after sowing (DAS). The experiment at ICRISAT Center received a pre-plant broadcast application of 40 kg ha⁻¹ of N and 17 kg ha⁻¹ of P and a topdressing of ca. 40 kg N ha⁻¹ at 20 DAS. The experiment at Hisar received 40 kg N and 17 kg P ha⁻¹ pre-plant and ca. 20 kg N ha⁻¹ topdressed at 20 DAS.

The second experiment (Experiment 2) contained 225 entries: (a) 46 random S₁ lines each from the C0 and the C1 of Higrop and Senpop when selection included consideration of bloom date and grain yield data (S₁ lines from sole GI1 selection not included), (b) 26 random BC₁ F₂ lines from the mating of the weedy relative from Senegal to the F₂ of ICMV 87901 x ICMV 82132, and (c) 15 open-pollinated and F₁ hybrid check varieties. The entries were evaluated in a 15 x 15 lattice design with two replications at ICRISAT Center and three replications at Hisar. Planting occurred on 14 July at ICRISAT Center and 4 July at Hisar. A plot consisted of two 4-m rows with 75 cm between rows. Seedlings were

thinned to 10-cm spacings within rows. The experiment at ICRISAT Center was irrigated twice after flowering occurred, whereas at Hisar, the experiment was irrigated throughout the season. Soil fertilization at ICRISAT Center and Hisar was the same as described above for Experiment 1. The traits measured on each plot for both experiments are presented in Table 1.

Table 1. Traits measured on population-generations and computation traits not measured directly.

Trait	Abbreviation	Calculation	Units
<u>Reported traits:</u>			
Bloom date	BD		d
Grain yield	GY	GW/PSZ2	g m ⁻²
Growth index 1	GI1	(SW1/PSZ1)/(BD + 10)	g m ⁻² d ⁻¹
<u>Traits used for calculations:</u>			
Plot size for GI1	PSZ1		m ²
Plot size at maturity	PSZ2		m ²
Straw weight at BD + 10	SW1		g m ⁻²
Grain weight	GW		g plot ⁻¹

Statistical Analysis

The two evaluation experiments were summarized separately and data for each trait were subjected to an analysis of variance.

For Experiment 1, all effects were considered fixed, except locations, which were random. The entry x location mean square was tested against the error means square, and when significant, was used to compute an LSD to test for differences between C0 and C1 for a trait for each gene pool (Steele and Torrie, 1980).

For Experiment 2, analyses of variance were performed using the statistical program PLABSTAT (Utz, 1987) on data from each location separately to determine lattice efficiencies. Because lattice efficiencies were low (100 - 110%), the data were analyzed as a randomized complete block design using the statistics program, SAS (SAS, 1987). Locations and lines within cycles were considered random, and cycles of selection were fixed. In most instances, direct F-tests were made to determine if cycle means were different. When this was not possible, an approximate F-test was performed using the method of Satterthwaite (1946). Analyses of variance were performed on lines from cycles of selection for each trait in each gene pool. Estimates of genetic variance components for the traits and genotype x location interaction variance components were computed for the CO and C1 of Higrop and Senpop by equating their expectations with means squares from the analyses of variance. Variance components were considered significant when they were greater than two times their standard errors (Hallauer and Miranda, 1985).

Broad-sense heritabilities for the traits were estimated as:

$$h^2 = \sigma_g^2 / \sigma_{ph}^2$$

where σ_g^2 and σ_{ph}^2 are genotypic and phenotypic variances, respectively. Upper and lower 95% confidence intervals for h^2 were calculated by the method of Knapp et al. (1985).

RESULTS AND DISCUSSION

Population Means

The midparent of ICMV 87901 x ICMV 82132 is the expected mean of the base population into which high G11 gene from the exotic parents were introgressed to form the Higrop and Senpop gene pools. G11 in C0 populations of both gene pools was greater than the midparent of ICMV 87901 x ICMV 82132 (Table 2). In Higrop, G11 was significantly greater by 2.7 g m⁻² d⁻¹ or 19% than the midparent, and in Senpop, G11 was greater by 1.4 g m⁻² d⁻¹ or 10% than the midparent value. These results concur with previous studies which demonstrated that exotic germplasm can be useful sources of genes for increasing vegetative growth index (GI) in oat (Cox and Frey, 1984; Gupta et al., 1986; Takeda and Frey, 1979, 1987) and pearl millet (Bramel-Cox et al., 1986). For both gene pools, bloom date (BD) was significantly later than the midparent, 3.1 d for Higrop and 7.7 d for Senpop. Grain yield (GY), however, was lower in both gene pools, by 9% and 2% of the midparent in Higrop and Senpop, respectively.

C0 and C1 means for BD, GY, and G11 in Higrop were not significantly different (Table 2). BD and G11 in Higrop decreased (4% and 3% of the C0 mean, respectively), and GY increased (5% of the C0 mean). For Senpop, BD was significantly decreased 4.8 d or 8% of the C0 mean, and G11 was significantly increased 3.2 g m⁻² d⁻¹ or 20% of the C0 mean. A non-significant increase in GY (19% of the C0 mean)

Table 2. Means of C_0 and C_1 for Higrop and Senpop for bloom date, grain yield, and vegetative growth index evaluated at three locations in India in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	$g\ m^{-2}$	$g\ m^{-2}\ d^{-1}$
<u>Higrop</u>			
C_0	53.3	221.1	17.1
C_1	51.4	231.0	16.6
SGI C_1	54.3	206.0	17.4
% of C_0	-4.0	5.0	-3.0
<u>Senpop</u>			
C_0	58.1	242.8	15.8
C_1	53.3*	286.4	19.0*
SGI C_1	54.5	250.4	18.0
% of C_0	-8.0	19.0	20.0
<u>Checks</u>			
ICMV 87901	48.2	239.4	12.6
ICMV 82132	52.6	256.6	16.2
LSD(0.05)	3.2	86.0	3.2

*Indicates significance at the 0.05 level.

occurred in Senpop. When progress occurred in Higrop, the percentage increase generally agreed with previous reports of progress from recurrent selection in pearl millet (Khadr, 1977; Rattunde et al., 1989), as well as for other crop species (Hallauer, 1985; Frey et al., 1988). In contrast, progress in Senpop generally was greater than progress previously reported from one cycle of recurrent selection.

Not only were direction, magnitude, and percent of change from C0 to C1 more favorable in Senpop than Higrop, but Senpop also appeared to be more efficient for utilizing a given growth duration. The interval from BD to grain maturity in pearl millet is relatively constant (Fussell and Pearson, 1978), so two pearl millet genotypes with equal bloom dates also should have equal maturity dates, and equal growth durations. Means for BD for Higrop C0 and Senpop C1 were both 53.3 d, but Senpop C1 produced 55.1 g m² more grain and had a GI1 2.4 g m² d⁻¹ greater than did Higrop C0.

When only GI1 was selected (i.e., SGI C1), BD was later and GY was lower than the C1 populations when BD and GY data were considered during selection. In SGI C1, GI1 increased in both gene pools (Table 2). For Higrop, the SGI1 selection increased GI1 0.3 g m² d⁻¹, whereas for Senpop, it increased 2.2 g m² d⁻¹. In neither gene pool was GI1 for SGI C1 significantly better than when GY and BD were considered during selection (i.e., Higrop and Senpop C1). Selecting parents with acceptable GY and BD, however, did have a positive effect in both gene pools. The C1 in Higrop was 3 d earlier and had a 25 g m² greater GY

than the SGI C1 in Higrop. The C1 in Senpop was 1 d earlier and had a 36 g m⁻² greater GY than the SGI C1.

Takeda and Frey (1987) practiced selection via independent culling for different combinations of harvest index, GI, and unit straw weight on oat lines from A. sativa L. x A. sterilis L. matings. They found that a 2% selection intensity solely for GI increased this trait 31% above the A. sativa parent CI 7463 and 27% above the parent CI 8044. However, the selected lines were tall and late. Gupta et al. (1986) found that selection solely for GI in oat caused inconsistent grain yield changes and the genetic variation for GI was exhausted after the second cycle of selection. In those studies, intense selection solely for GI gave dramatic increases in this trait but these selected oat lines were agronomically unacceptable. My results with pearl millet corroborate those found with oat. That is, selection solely for GI in pearl millet populations caused undesirable changes in the important agronomic traits, GY and BD. Takeda and Frey (1977) found that a 25% selection intensity for harvest index, followed by an 8% selection intensity for GI was the best selection regime in oat for increasing both its GI and grain yield. Takeda and Frey (1977) discussed the importance of considering both assimilate productivity (i.e., GI) and assimilate partitioning (i.e., harvest index) when the goal was high yielding oat lines with desirable agronomic characteristics. Likewise with pearl millet, selection for greater assimilate productivity (i.e.,

G11) and greater assimilate partitioning (i.e., GY) gave increased G11 and acceptable levels for agronomic traits.

Cycle means for the gene pools when grown at ICRISAT Center, Hisar, and Bhavanisagar are presented in Tables 3 - 5. In Higrop, BD, GY, or G11 were not significantly different in the C0 and C1 at any site. Because parents selected to form the C0 and C1 populations of Higrop and Senpop were based upon data from both Hisar and ICRISAT Center, progress for G11 was expected at both sites and only at ICRISAT Center were changes in BD, GY, and G11 in the desired direction.

In contrast to Higrop, improvement occurred in Senpop at all sites and for all traits. For Senpop, BD was significantly decreased 8.5 d or 12% of the C0 mean at Hisar and 3.0 d or 6% of the C0 mean at Bhavanisagar. Though non-significant, improvement in GY ranged from 9% of the C0 mean at ICRISAT Center to 17% of the C0 mean at Bhavanisagar. Only at Hisar was G11 significantly increased, by 5.8 g m⁻² d⁻¹ or 51% of the C0 mean.

Trait Means for Random S₁ Lines

Improvement occurred in both gene pools and for all traits when data from the S₁-lines was combined over sites (Table 6). In Higrop, GY increased significantly by 17.9 g m⁻² or 10% of the C0 mean. Though non-significant, BD was earlier (5% of the C0 mean) and G11 was greater (7% of the C0 mean) in Higrop. In Senpop, cycle means for BD, GY and G11 were not significantly different. However, BD was earlier (8% of

Table 3. Means of C_0 and C_1 for Higrop and Senpop for bloom date, grain yield, and vegetative growth index evaluated at ICRISAT Center in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	$g\ m^{-2}$	$g\ m^{-2}\ d^{-1}$
<u>Higrop</u>			
C_0	53.5	251.8	6.6
C_1	51.8	269.5	8.9
SGI C_1	53.5	259.0	9.4
% of C_0	-2.8	7.0	34.7
<u>Senpop</u>			
C_0	56.5	355.8	6.8
C_1	53.8	387.7	7.4
SGI C_1	53.3	337.9	7.6
% of C_0	-4.8	9.0	8.8
<u>Checks</u>			
ICMV 87901	47.8	274.2	4.4
ICMV 82132	53.8	272.5	7.8
LSD(0.05)	2.9	135.0	3.1

Table 4. Means of C_0 and C_1 for Higrop and Senpop for bloom date, grain yield, and vegetative growth index evaluated at Hisar in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	$g\ m^{-2}$	$g\ m^{-2}\ d^{-1}$
<u>Higrop</u>			
C_0	61.3	192.2	18.7
C_1	56.5	160.5	16.3
SGI C_1	62.8	129.2	16.0
% of C_0	-7.8	-16.5	-12.3
<u>Senpop</u>			
C_0	69.8	121.7	11.4
C_1	61.3*	178.2	17.2*
SGI C_1	63.8*	118.2	18.3*
% of C_0	-12.2	46.4	50.4
<u>Checks</u>			
ICMV 87901	54.3	199.9	12.1
ICMV 82132	59.5	217.7	15.4
LSD(0.05)	4.5	99.2	5.4

*Indicates significance at 0.05 level.

Table 5. Means of C_0 and C_1 for Higrop and Senpop for bloom date, grain yield, and vegetative growth index evaluated at Bhavanisagar in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	g m^{-2}	$\text{g m}^{-2} \text{ d}^{-1}$
<u>Higrop</u>			
C_0	45.3	249.3	26.1
C_1	46.0	263.1	24.3
SGI C_1	46.8	229.8	26.5
% of C_0	1.6	5.5	-7.1
<u>Senpop</u>			
C_0	48.0	250.8	29.4
C_1	45.0*	293.3	32.2
SGI C_1	46.5*	273.8	27.9
% of C_0	6.3	17.0	9.6
<u>Checks</u>			
ICMV 87901	42.5	244.0	21.3
ICMV 82132	44.5	279.7	25.5
LSD(0.05)	1.3	83.2	5.4

*Indicates significance at 0.05 level.

Table 6. Means of S_1 lines from Higrop and Senpop C_0 and C_1 for bloom date, grain yield, and vegetative growth index evaluated at two locations in India in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	$g\ m^{-2}$	$g\ m^{-2}\ d^{-1}$
<u>Higrop</u>			
C_0	59.0	193.7	12.7
C_1	56.2	211.6*	13.6
% of C_0	-4.7	9.2	7.1
<u>Senpop</u>			
C_0	62.2	188.6	13.0
C_1	57.4	220.4	13.6
% of C_0	-7.7	16.9	4.6

*Indicates significance at 0.05 level.

the C0 mean), and GY and GI1 were increased (17% and 5% of the C0 mean, respectively) in Senpop.

When grown at ICRISAT Center, cycle means for BD, GY, and GI1 in Higrop and Senpop were not significantly different (Table 7). In Higrop, BD became slightly earlier (1% of the C0 mean) and GY increased (2% of the C0 mean), but GI1 decreased (3% of the C0 mean). In Senpop, BD, GY, and GI1 all were decreased (2%, 6%, and 4%, respectively, of the C0 mean). Environmental conditions for pearl millet production at ICRISAT Center were not favorable in 1991 and probably this is the primary cause of no progress for GI1 at this site. Poor seedling emergence, caused by root feeding insects, adversely affected the trial. One replication of this trial at ICRISAT Center was discarded due to the irregular plant placement. In fact, GI1 values recorded for Higrop and Senpop at ICRISAT Center are substantially less than those (10.8 - 14.3 g m⁻² d⁻¹) reported by Bramel-Cox et al. (1986) who studied similar pearl millet germplasm that also was evaluated in the same (rainy) season as Higrop and Senpop were evaluated.

At Hisar, significant progress occurred for all traits of both gene pools (Table 8). In Higrop, BD was decreased 4.3 d (7% of the C0 mean), GY was increased by 26.7 g m⁻² (15% of the C0 mean) and GI1 was increased by 1.7 g m⁻² d⁻¹ (11% of the C0 mean). In Senpop, BD was decreased by 7.2 d (11% of the C0 mean) and GY was increased by 62 g

Table 7. Means of S₁ lines from Higrop and Senpop C₀ and C₁ for bloom date, grain yield, and vegetative growth index evaluated at ICRISAT Center in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	g m ⁻²	g m ⁻² d ⁻¹
<u>Higrop</u>			
C ₀	54.3	211.5	8.1
C ₁	53.8	216.3	7.9
% of C ₀	-1.0	2.3	-2.5
<u>Senpop</u>			
C ₀	55.7	228.9	8.4
C ₁	54.4	215.5	8.1
% of C ₀	-2.3	-5.9	-3.5

Table 8. Means of S₁ lines from Higrop and Senpop C₀ and C₁ for bloom date, grain yield, and vegetative growth index evaluated at Hisar in 1991.

Cycle	Traits		
	BD	GY	GI1
	DAE	g m ⁻²	g m ⁻² d ⁻¹
<u>Higrop</u>			
C ₀	62.1	181.8	15.7
C ₁	57.8*	208.5**	17.4*
% of C ₀	6.9	14.6	10.9
<u>Senpop</u>			
C ₀	66.6	161.6	16.1
C ₁	59.4**	223.6**	17.2*
% of C ₀	10.8	38.4	7.2

*,**Indicates significance at 0.05 and 0.01 levels, respectively.

*Significant at 0.08% level.

(38% of the C0 mean). GI1 in Senpop was increased by $1.1 \text{ g m}^{-2} \text{ d}^{-1}$ or 7% of the C0 mean (significant at the 8% level).

Trait Variance and Heritability Estimates

In Higrop, significant genetic variance occurred in C0 for BD and in C1 for BD and GI1 (Table 9). In Senpop, significant genetic variance occurred for BD in C0 and C1, and for GY in C1 (Table 10). In both gene pools, genetic variance for GY decreased with selection, whereas for GI1, it increased. For BD, genetic variance increased in Higrop, and in Senpop it decreased.

Despite the 12° difference in latitude between ICRISAT Center and Hisar, few instances of significant Genotype x Environment (GE) variance occurred. For Higrop, GE variance was significant for BD in the C1, whereas for Senpop, GE variance was significant for BD in the C0 and C1 and for GY in the C1. Begg and Burton (1971) found GE effects for BD of pearl millet when grown under different daylengths and temperatures. The GE variance decreased from C0 to C1 for GI1 in Higrop, and for all traits in Senpop. Thus, one cycle of recurrent selection may have increased the stability of GI1 in both gene pools.

Heritabilities in Higrop and Senpop were significant for BD in the C0 and C1 and for GI1 in the C1. In Senpop, heritability for GY was significant in the C0 and C1, but in neither cycle of Higrop. For both gene pools, heritabilities decreased for BD and increased for GI1 from the C0 to C1. For GY, heritability in Higrop decreased with selection,

Table 9. Genotypic (σ^2_g) and genotype x environment (σ^2_{ge}) variances and heritabilities (h^2) and their standard errors for bloom date, grain yield, and vegetative growth index estimated from random S_1 lines from Higrop C_0 and C_1 evaluated at two locations in 1991.

Estimate	Traits		
	BD	GY	GI1
$C_0 \sigma^2_g$	11±3*	620±388	0.8±1.3
$C_1 \sigma^2_g$	21±6*	306±328	2.5±1.1*
$C_0 \sigma^2_{ge}$	4±3	164±566	2.0±2.1
$C_1 \sigma^2_{ge}$	10±3*	798±525	0.8±1.4
$C_0 h^2$	69*	39	18
$C_1 h^2$	76*	22	51*

*Indicates significance at 0.05 level.

Table 10. Genotypic (σ_g^2) and genotype x environment (σ_{ge}^2) variances and heritabilities (h^2) and their standard errors for bloom date, grain from random S_1 lines from Senpop C_0 and C_1 evaluated at two locations in 1991.

Estimate	Traits		
	BD	GY	GI1
$C_0 \sigma_g^2$	17±5*	1113±654	1.0±1.4
$C_1 \sigma_g^2$	14±4*	978±479*	1.6±1.0
$C_0 \sigma_{ge}^2$	10±5*	1717±865	3.0±2.3
$C_1 \sigma_{ge}^2$	9±3*	602±605	0.2±1.4
$C_0 h^2$	73*	41*	19
$C_1 h^2$	69*	48*	40*

*Indicates significance at 0.05 level.

whereas in Senpop it increased with selection. Heritabilities for BD were high (i.e., ca. 70%) and for GY and GI1 they were moderate (i.e., ca. 45%). Heritabilities in Higrop and Senpop are slightly lower than those found by Rattunde et al. (1989), who reported heritabilities in four pearl millet composites of ca. 96% for BD and ca. 70% for GY and GI2 (i.e., GI measured at maturity, not 10 d after flowering). However, the heritabilities of Rattunde et al. (1989) were computed from data from one location, and likely were biased upward by GE interactions. The genetic variance and heritabilities suggest that future selection for improved BD, GY, and GI1 is likely possible in Higrop and Senpop.

In summary, Higrop and Senpop possessed greater GI1 than the midparent value of ICMV 87901 x ICMV 82132. Regardless of whether selection was based solely upon GI1 (i.e., SGI1) or on GI1, BD, and GY, one cycle of S_1 -line recurrent selection increased GI1 in both Higrop and Senpop. However, selection solely for GI1 caused associated changes of later maturity and lower GY than when GI1, GY, and BD were selected. Thus, inclusion of BD and GY data during selection was critical for simultaneously increasing GI1 and maintaining acceptable levels of BD and GY. The C1 populations of both Higrop and Senpop had medium maturity and high GY and GI1. However, Senpop appears to be the superior gene pool for making genetic gains. After only one cycle of selection, Senpop C1 had 12% greater GY and 17% greater GI1 than ICMV 82132, the parent variety with highest GY and GI1. In contrast, Higrop C1 had 10% lower GY and only 2% greater GI1 than ICMV 82132.

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PAPER III. INDIRECT RESPONSES AND TRAIT ASSOCIATIONS AMONG
AGRONOMIC TRAITS FROM S_1 -LINE RECURRENT SELECTION FOR
INCREASED VEGETATIVE GROWTH INDEX IN PEARL MILLET
(PENNISETUM GLAUCUM (L.) R. Br.)

ABSTRACT

The Higrop and Senpop gene pools were formed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to assess the efficacy of recurrent selection for increased vegetative growth index (GI) for increasing grain yield in pearl millet. In this study, the correlated responses which occurred after one cycle of recurrent selection in Higrop and Senpop for increased GI were assessed by using 46 S₁ lines in C0 and in C1 of each gene pool, and evaluated at ICRISAT Center and Hisar in 1991. Bloom date (BD), grain yield (GY), GI measured at 10 d after BD (GI1) and eleven unselected traits were measured. Selection in Higrop significantly increased GY (18 g m²) and decreased panicle length (2 cm). Selection in Senpop significantly increased panicle length, panicle girth, and panicles per plant by 2 cm, 1.7 mm, and 0.3 panicles plant⁻¹, respectively, and significantly decreased plant height by 10.2 cm. Substantial non-significant increases occurred for panicles per plant in Higrop (13.6% of the C0 mean) and harvest index in Senpop (16.4% of the C0 mean). Heritabilities in Higrop increased for all traits from C0 to C1, except for GY, GI2, panicle length, and stem girth. Heritabilities in Senpop decreased from C0 to C1 more frequently than they increased, ranging from 5 - 36% less in C1 than in C0. Phenotypically, GY was correlated (P<0.01) with panicle yield, harvest index, and threshing percent in both cycles of the gene pools, while genotypic correlations were high for GY with panicle yield, panicles per plant, and harvest index in

Higrop and Senpop. Phenotypically, GI1 was correlated ($P < 0.01$) in C0 and C1 of both gene pools only with plant height and genotypically, GI1 was negatively correlated with panicle girth, panicles per plant, and harvest index in both gene pools. In both of the gene pools selection resulted in decreased BD and increased GY and GI1, likely because the selection procedure used in Higrop and Senpop included culling of S_1 lines which had high GI1 but low GY or late BD. Future selection in Higrop and Senpop for high GI1 and GY and low BD should be successful, and few, if any, undesirable correlated changes are likely to occur in unselected agronomic traits.

INTRODUCTION

Selection for increased vegetative growth index (GI) has been proposed as a method for improving grain yield in cereals that have a short growth duration (Takeda and Frey, 1976, 1977). Because the growth duration of pearl millet in India is short, ranging from 70 to 100 days (Virmani et. al, 1982), its grain yield may benefit from selection for increased vegetative growth index. Previously, Bramel-Cox et al. (1984) demonstrated that genes for high GI measured at 10 d after bloom date (i.e., GI1) exist in the primary gene pool of pearl millet and recently gene pools with high GI1, Higrop and Senpop, were formed (Lynch, 1993). After one cycle of recurrent selection in those gene pools, GI1 and grain yield were increased and the number of days to flowering was decreased (Lynch, 1993).

When selection is practiced for one or more traits in a gene pool, correlated changes in unselected, but agronomically important, traits can occur due to genetic linkage and/or pleiotropy. Selection for GI in oat has caused correlated changes in unselected traits (Gupta et al., 1986; Takeda and Frey, 1987). Although selection for increased GI has been conducted in pearl millet (Bramel-Cox et al., 1986), correlated responses were not reported.

One objective of this study was to quantify changes that occurred in unselected traits after one cycle of S_1 -line recurrent selection for increased GI1 in the pearl millet gene pools, Higrop and Senpop. Additionally, phenotypic and genotypic correlations of GI1 and grain

yield with several unselected traits in the C0 and C1 of Higrop and Senpop are presented.

MATERIALS AND METHODS

Gene Pool Development

The plant populations used for this study were Higrop (High Growth Rate Population) and Senpop (Senegal Population), gene pools formed at The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, to evaluate the potential of exotic germplasm for increasing G11 of cultivated pearl millet (Bramel-Cox et al., 1986).

The formation of Higrop and Senpop began in the March - May season, 1988, when four landraces, two wild subspecies [ssp. monodii (Maire) Brunken], and two weedy subspecies [ssp. stenostachyum (Klotzsch ex A. Br. and Bouche) Brunken] of pearl millet, collected in India and Africa, were crossed onto an F₂ population. The F₂ was from the mating ICMV 87901 x ICMV 82132. The ICMV parents were ICRISAT varieties with medium maturity and high grain yield. In the November - February season, 1988-89, the F₁s from wild and weedy ssp. matings were backcrossed to the F₂ and the F₁s involving the landraces were random mated. In the March - May season, 1989, the seeds from the random matings and BC₁ F₁s were space-planted and selfed to form S₁ lines and BC₁ F₂ lines. In the July - October season, 1989, 38 S₁ or BC₁ F₂ lines from each landrace mating and each wild and weedy ssp. BC₁ mating, along with 20 checks, were evaluated in an 18 x 18 lattice experiment with two replications in a field at ICRISAT Center. The 20 S₁ or BC₁ F₂ lines from this trial that had the highest G11 (Bramel-Cox et al., 1984) and acceptable grain

yields and maturities were intermated to initiate the Higrop gene pool. Next, a BC_1 mating which involved a weedy accession from Senegal was judged to be the best of the eight matings on the basis of the means of its 38 $BC_1 F_2$ lines for G11, grain yield, and maturity. The 20 $BC_1 F_2$ lines from this mating with the highest G11's and acceptable grain yields and maturities were intermated to initiate the Senpop gene pool.

To intermate the 20 S_1 and $BC_1 F_2$ lines selected to initiate Higrop, a bulk of pollen from n plants in each of the 20 lines was used to pollinate n plants in each of the 20 lines. This intermating plan was continued daily until ca. 25 plants had been pollinated in each of the 20 selected lines. A plant was used only once as a male or female. Seeds from a crossed panicle formed a half-sib family. $BC_1 F_2$ lines selected to form Senpop were intermated via a diallel mating plan in which the pollen from one plant within a line was used to pollinate one plant in a different line. The crossing was continued until one plant within each $BC_1 F_2$ line had been crossed with one plant in each of the remaining 19 $BC_1 F_2$ lines. A plant was used only once as a male or female. This crossing procedure was executed twice to produce 380 full-sib progenies.

At maturity, the crossed panicles were cut, sun-dried, and threshed individually. The C_0 populations were formed by bulking ca. 10 g of seed from (a) each of the ca. 500 half-sib progenies in Higrop and (b) each of the ca. 380 full-sib progenies in Senpop.

Recurrent Selection Procedure

The single cycle of recurrent selection conducted in Higrop and Senpop, consisted of three phases: (1) Field evaluation of random S_1 lines, (2) recombination of the 20 S_1 lines that had high G11 and acceptable grain yields and numbers of days to flowering, and (3) production of random S_1 lines.

In July - October 1990 134 random S_1 progenies from the C_0 of each gene pool plus 10 check entries were evaluated in a 12 x 12 triple lattice design at two locations in India. Planting dates were on 25 June at ICRISAT Center and 9 July at Hisar, Harayana. A plot was two 4-m rows spaced 75 cm apart. At ca. 14 days after emergence, seedlings were thinned to approximately one plant per 10 cm of row. Each experiment received a pre-plant broadcast application of 40 and 17 kg ha^{-1} of nitrogen and phosphorus, respectively. Side-dressings of ca. 40 and 20 kg ha^{-1} of N (applied as urea), at ICRISAT Center and Hisar, respectively, were made 20 days after emergence. Plots were hand-weeded twice.

During November - March, 1990-91, the 20 S_1 lines with high G11 and acceptable grain yields and bloom dates from each gene pool were intermated. As described for making the C_0 populations, half-sib matings were made for recombining the selected lines in Higrop and full-sib matings were made for recombining the selected lines in Senpop. At maturity (Fussel and Pearson, 1978) all crossed panicles within a gene

pool were harvested, threshed individually, and ca. 10-g seed lots from all progenies were bulked to produce the C1 population.

During February - May, 1991, ca. 300 plants from C0 and C1 populations of each gene pool were grown at wide spacing (50 cm between plants), and all panicles on a plant were selfed. At maturity, all selfed panicles of a plant were harvested, dried, and threshed. This bulk of seed from an S_0 plant represented an S_1 line.

Evaluation of Progress From Selection

An experiment was conducted during July - October, 1991, to evaluate progress from selection for increased GI1. The experiment contained 225 entries: (a) 46 random S_1 lines each from the C0 and the C1 of Higrop and Senpop, (b) 26 random $BC_1 F_2$ lines from the mating of the weedy relative from Senegal to the F_2 of ICMV 87901 x ICMV 82132, and (c) 15 open-pollinated and F_1 hybrid check varieties. The entries were evaluated in a 15 x 15 lattice design with two replications at ICRISAT Center (17°N), and three replications at Hisar (29°N). Planting occurred on 14 July at ICRISAT Center and 4 July at Hisar. A plot consisted of two 4-m rows with 75 cm between rows. Seedlings were thinned to 10-cm spacings within rows. The experiment at ICRISAT Center was irrigated twice after flowering occurred, whereas at Hisar, the experiment was irrigated throughout the season. The experiment at ICRISAT Center received a pre-plant broadcast application of 40 kg ha⁻¹ of N and 17 kg ha⁻¹ of P and a topdressing of ca. 40 kg N ha⁻¹ at 20 DAS.

The experiment at Hisar received 40 kg N and 17 kg P ha⁻¹ pre-plant and ca. 20 kg N ha⁻¹ topdressed at 20 DAS. The traits measured on each plot for both experiments are presented in Table 1.

Table 1. Traits measured on S₁ lines from cycles of selection in Higrop and Senpop that were reported or used in calculations.

Trait	Abbreviation	Calculation	Units
<u>Reported traits:</u>			
Bloom date	BD		d
Panicle yield	PY	PW/PSZ2	g m ⁻²
Grain yield	GY	GW/PSZ2	g m ⁻²
Biomass	BM	(SW2 + PW)/PSZ2	g m ⁻²
Growth Index 1	GI1	(SW1/PSZ1)/(BD + 10)	g m ⁻² d ⁻¹
Growth Index 2	GI2	(SW2/PSZ2)/(BD + 10)	g m ⁻² d ⁻¹
Harvest index	HI	GW/BM	%
Threshing percent	TP	GW/PW	%
Plant height	PH		cm
Panicle length	PL		cm
Panicle girth	PG		mm
Stem girth	SG		mm
Leaf width	LW		mm
Panicles per plant	PP	PaC/PC	# plant ⁻¹
<u>Traits used for calculations:</u>			
Panicle weight	PW		g plot ⁻¹
Grain weight	GW		g plot ⁻¹
Plot size for GI1	PSZ1		m ²
Plot size at maturity	PSZ2		m ²
Straw weight at BD + 10	SW1		g plot ⁻¹
Straw weight at maturity	SW2		g plot ⁻¹
Panicle count	PaC		# plot ⁻¹
Plant count	PC		# plot ⁻¹

Statistical Analysis

Analyses of variance were performed using the statistical program PLABSTAT (Utz, 1987) on data from each location separately to determine lattice efficiencies. Because lattice efficiencies were low (100 - 110%), the data were analyzed as a randomized complete block design using the statistics program, SAS (SAS, 1987). Locations and lines within cycles were considered random, and cycles of selection were fixed. In most instances, direct F-tests were made to determine if differences between cycle means existed. When this was not possible, an approximate F-test was performed using the method of Satterthwaite (1946). Analyses of variance were performed on individual cycles of selection for each trait. Estimates of genetic variance components for the traits and genotype x location interaction variance components were computed for the CO and Cl of Higrop and Senpop by equating their expectations with means squares from the analyses of variance. Variance components were considered significant when they were greater than two times their standard errors (Hallauer and Miranda, 1985).

Broad-sense heritabilities for the traits were estimated as:

$$h^2 = \sigma_g^2 / \sigma_{ph}^2$$

where σ_g^2 and σ_{ph}^2 are genotypic and phenotypic variances, respectively.

All heritabilities have a reference unit of two locations and two or three replications per location. Upper and lower 95% confidence intervals for h^2 were calculated by the method of Knapp et al. (1985).

Phenotypic and genotypic correlations for vegetative growth index and grain yield with unselected agronomic traits were calculated on an entry mean basis within cycles of selection by using the formula:

$$r = \frac{\text{cov}(xy)}{\sqrt{\text{var}(x) * \text{var}(y)}},$$

where Cov(xy) is the phenotypic or genotypic covariance between traits X and Y, and Var(x) and Var(y) are the phenotypic or genotypic variances for traits x and y, respectively.

RESULTS

Trait Means

Selection increased GIl and GY and decreased BD in both gene pools and resulted in generally favorable changes for the unselected traits (Table 2). Changes from C0 to C1 in Higrop were an 18 g m² increase in GY and a 2 cm decrease in PL, both of which were significant. Significant changes occurred from C0 to C1 in Senpop for PL, PG, and PP. The increases were 2 cm, 1.7 mm, and 0.3 panicles plant⁻¹, respectively. PH in Senpop decreased significantly by 10.2 cm. Substantial correlated responses occurred in both gene pools for PP, which increased by 13.6% and 14.3% of the C0 mean in Higrop and Senpop, respectively. In Senpop, HI increased 16.4% of the C0 mean. Other lesser correlated responses in both gene pools occurred with decreases in PH, SG, and LW.

For cereals, the product of GI and growth duration equals BM and HI represents how BM is partitioned between reproductive and vegetative portions of the plant (Takeda and Frey, 1977). Pearl millet lines with equal BDs generally possess equal growth durations (Fussel and Pearson, 1978). Thus, the 5% decrease in BD of Higrop represents a decrease in its growth duration. However, because GI increased, BM in Higrop increased by 3%. The increase in GY for Higrop occurred because HI and TP increased. Increased HI caused more of BM to be located in panicles, and increased TP caused more of panicle weight to occur as grain. Although GIl in Senpop did increase, this was not sufficient to counteract the shorter growth duration. The result was that BM

Table 2. Means of S_1 lines from Higrop and Senpop C_0 and C_1 for several traits evaluated at two locations in India in 1991.

Genepool	Traits							
	BD	PY	GY	BM	GI1	GI2	HI	TP
	DAE	g m ²			g m ² d ⁻¹		%	
<u>Higrop</u>								
C_0	59.0	275.9	193.6	852.4	12.7	8.5	24.8	69.9
C_1	56.2	298.1	211.6*	877.7	13.6	9.1	25.9	70.1
% of C_0	-4.7	8.0	9.3	3.0	7.1	7.1	4.4	0.3
<u>Senpop</u>								
C_0	62.2	265.0	188.6	950.2	13.0	9.2	23.2	70.4
C_1	57.4	307.2	220.4	905.2	13.6	8.8	27.0	71.3
% of C_0	-7.7	15.9	16.9	-4.7	4.6	-4.3	16.4	1.3

*,**Indicate significance at the 0.05 and 0.01 levels respectively.

Table 2. Continued.

Genepool	Traits					
	PH	PL	PG	SG	LW	PP
	<u>cm</u>		<u>mm</u>			<u># plant⁻¹</u>
<u>Higrop</u>						
C ₀	207.4	22.5	27.4	11.0	38.2	2.2
C ₁	205.4	20.5**	26.9	10.8	37.0	2.5
% of C ₀	-1.0	-8.9	-1.8	-1.8	-3.1	13.6
<u>Senpop</u>						
C ₀	211.6	22.0	26.0	11.4	39.7	2.1
C ₁	201.4**	22.5*	27.7*	11.0	39.0	2.4**
% of C ₀	-4.8	2.3	6.5	-3.5	-1.7	14.3

decreased 5% from C0 to C1 in Senpop. However, the 16% increase in HI and the 1% increase in TP caused GY to increase with selection, despite the reduced BM in Senpop C1.

Genotypic Variance and Heritabilities

Genotypic variances were significant in Higrop C0 for BD, PH, PL, and PG, and in C1 for all traits except PY, GY, GI2, TP, and SG (Table 3). Genotypic variance was significant in Senpop C0 for all traits, except PY, GY, GI1, TP, SG, and PP, and in Senpop C1, for all traits except BM, GI1, GI2, TP, and SG (Table 4). Even though significant genotypic variances for GY and GI1 were not detected among the lines, means for these traits in Higrop increased 9.3 and 7.1%, respectively from C0 to C1 (Table 2). Significant genotypic variation for these traits obviously was present. The lack of significant genotypic variance may have resulted because only 46 S₁ lines from a cycle of selection were evaluated, whereas for the selection experiments, 134 S₁ lines from a cycle of selection were evaluated. Genotypic variance increased from C0 to C1 in both gene pools for GI1, HI, TP and decreased for GY, GI2, PL, PG, and SG.

In Higrop C0, genotype x environment variance (GE) was significant for TP, and in C1 it was significant for BD, PH, and PL. In Senpop C0, GE was significant for PY, HI, and PH, and in C1 for BD and PG. Generally, GE for the traits in both gene pools were reduced from C0 to

Table 3. Genotypic (σ_g^2) and genotype x environment (σ_{ge}^2) variances and heritabilities (h^2) and their standard errors for several traits estimated from random S_1 lines from Higrop C_0 and C_1 evaluated at two locations in 1991.

	Traits							
	BD	PY	GY	BM	GI1	GI2	HI ^a	TP ^a
$C_0 \sigma_g^2$	11±3*	566±658	620±388	12368±8024	0.8±1.3	2.1±1.3	7.9±4.2	1.5±9.2
$C_1 \sigma_g^2$	21±6*	485±490	306±328	13558±6194*	2.5±1.1*	1.4±0.8	8.1±3.7*	5.6±4.4
$C_0 \sigma_{ge}^2$	4±3	578±1099	164±566	12416±106156	2.0±2.1	-0.1±1.4	6.1±5.5	7.1±1.8*
$C_1 \sigma_{ge}^2$	10±3*	819±794	798±525	4333±7669	0.8±1.4	-0.1±1.1	8.4±5.3	-1.8±9.7
$C_0 h^2$	69.1*	22.4	38.7	37.4	17.6	48.3*	41.7*	4.7
$C_1 h^2$	75.5*	25.2	22.1	50.4*	51.0*	42.7	50.1*	38.3

^aActual value= σ_g^2 or $\sigma_{ge}^2 \times 10^{-4}$

*Indicates significance at 0.05 level.

Table 3. Continued

	Traits					
	PH	PL	PG	SG	LW	PP
$C_0 \sigma_g^2$	95±43*	6.3±1.7*	3.8±1.6*	0.15±0.09	3.6±2.7	0.02±0.04
$C_1 \sigma_g^2$	161±60*	4.2±1.2*	2.8±1.0*	-0.06±0.14	15.0±4.2*	0.17±0.07*
$C_0 \sigma_{gc}^2$	45±50	0.9±1.0	0.9±1.9	0.22±1.55	3.9±4.0	0.05±0.06
$C_1 \sigma_{gc}^2$	111±58*	1.5±0.7*	0.3±1.0	0.32±0.27	-3.7±3.2	0.07±0.07
$C_0 h^2$	50.6*	77.8*	53.4*	37.7	32.7	14.4
$C_1 h^2$	59.8*	76.5*	61.5*	14.1	75.5*	57.6*

Table 4. Genotypic (σ_g^2) and genotype x environment (σ_{ge}^2) variances and heritabilities (h^2) and their standard errors for several traits estimated from random S_1 lines from Senpop C_0 and C_1 evaluated at two locations in 1991.

	Traits							
	BD	PY	GY	BM	GI1	GI2	HI ^a	TP ^a
$C_0 \sigma_g^2$	17±5*	1737±1117	1132±654	39608±14791*	1.0±1.4	3.5±1.7*	15.0±5.5*	3.5±5.5
$C_1 \sigma_g^2$	14±4*	1476±726*	978±479*	15786±8799	1.6±1.0	3.1±2.0	18.3±5.4*	7.0±4.4
$C_0 \sigma_{ge}^2$	10±5	3258±1524*	1717±865	-19441±17688	3.0±2.3	-1.7±2.3	12.2±5.2*	8.7±9.5
$C_1 \sigma_{ge}^2$	9±3*	567±939	602±605	-11597±13630	0.2±1.4	3.6±3.3	4.8±3.7	5.4±6.3
$C_0 h^2$	73.0*	37.8	40.8*	59.6*	18.8	45.5*	60.2*	16.9
$C_1 h^2$	69.0*	47.4	47.5	42.7	40.4	37.9	38.5*	57.5*

^aActual value= σ_g^2 or $\sigma_{ge}^2 \times 10^{-4}$

*Indicates significance at 0.05 level.

Table 4. Continued

Genepool	Traits					
	PH	PL	PG	SG	LW	PP
$C_0 \sigma_g^2$	128±57*	6.9±1.9*	2.8±1.1*	0.19±0.16	8.8±2.9*	-0.05±0.08
$C_1 \sigma_g^2$	101±40*	2.9±1.0*	2.5±1.2*	0.16±0.14	7.1±3.0*	0.01±0.07
$C_0 \sigma_{ge}^2$	134±64*	2.1±1.1	1.0±1.2	0.32±0.25	1.8±2.6	0.29±0.15
$C_1 \sigma_{ge}^2$	59±41	1.7±0.9	2.9±1.4*	0.27±0.22	1.9±3.5	0.17±0.13
$C_0 h^2$	51.4*	77.7*	55.8*	39.6	65.9*	-23.6
$C_1 h^2$	57.5*	63.9*	49.0*	28.9	54.0*	5.0

C1, indicating that the selection for GI1 contributed to increased stability of the lines derived from these gene pools.

Heritabilities in Higrop increased for all traits from C0 to C1, except for GY, GI2, PL, and SG. In Higrop C1, heritabilities were high for BD, PL, and LW, low for PY, GY, TP, and SG, and moderate for the remaining traits. In Senpop heritabilities decreased from C0 to C1 more frequently than they increased, ranging from 5 - 36% less in C1 than in C0. In Senpop C1, heritabilities were moderate for all traits except for SG and PP, which were low. In both gene pools, heritabilities generally were lower than the values reported by Rattunde et al. (1989). However, their heritabilities were computed from a single location, which could cause them to be biased upward by genotype x environment interactions.

Phenotypic and Genotypic Correlations

Phenotypic and genotypic correlations for GY and GI1 with the other traits are presented in Tables 5 and 6, respectively. Phenotypically, GY was correlated ($P < 0.01$) with PY, HI, and TP in both cycles of the gene pools, and in Higrop C0 and C1 and Senpop C1, GY was correlated with BM. Similar correlations were reported by Bramel-Cox (1985), who found GY was positively correlated with HI (0.86) and TP (0.62), but negatively correlated with BD (-0.61). Genotypic correlations were high for GY with PY, PP, and HI in Higrop and Senpop. Negative genotypic

Table 5. Phenotypic and genotypic (lower value) correlations for grain yield of Higrop and Senpop with several agronomic traits in C0 and C1 when evaluated at two locations in 1991.

Trait	Higrop		Senspop	
	C0	C1	C0	C1
Bloom date	-0.24 -0.45	0.15 0.42	0.41** -0.36	-0.27 -0.10
Panicle yield	0.96** 1.07	0.90** 0.70	0.98** 0.99	0.96** 0.98
Biomass	0.39** 0.25	0.53** 0.63	0.28 0.54	0.37** 0.25
Vegetative growth index 1	-0.15 -0.71	0.30* 0.20	0.02 -0.84	0.14 -0.17
Vegetative growth index 2	0.21 0.12	0.35* 0.49	0.13 0.46	0.16 -0.05
Harvest Index	0.57** 0.79	0.44** 0.27	0.77** 0.91	0.69** 0.74
Threshing percent	0.39** 1.50	0.41** 0.24	0.48** 0.81	0.52** 0.55
Plant height	0.22 0.19	0.17 0.23	0.10 0.23	0.07 -0.07
Panicle length	0.45** 0.61	0.01 0.26	0.05 -0.01	0.13 -0.13
Panicle girth	0.22 0.23	0.04 0.03	0.07 -0.07	0.08 -0.09
Stem girth	0.36* 1.08	0.13 1.63	-0.13 -0.11	0.03 -0.09
Leaf width	0.21 0.21	0.27 0.67	-0.19 -0.15	-0.07 -0.51
Panicles per plant	0.12 -0.30	-0.14 -0.74	0.61** 1.05	0.34* 1.08

*, **Indicates significance at 0.05 and 0.01 levels, respectively.

Table 6. Phenotypic and genotypic (lower value) correlations for vegetative growth index 1 of Higrop and Senpop with several agronomic traits in C0 and C1 when evaluated at two locations in 1991.

Trait	Higrop		Senpop	
	C0	C1	C0	C1
Bloom date	0.04 0.33	0.29* 0.42	0.12 0.65	-0.01 0.11
Panicle yield	-0.14 -1.02	0.33* 0.23	0.10 -0.98	0.15 -0.07
Grain yield	-0.15 -0.71	0.30* 0.20	0.02 -0.84	0.14 -0.17
Biomass	0.31* 0.97	0.59** 0.78	0.05 -0.31	0.22 0.15
Growth index 2	0.40** 1.07	0.57** 0.86	0.06 -0.34	0.17 0.08
Harvest Index	-0.33* -1.28	-0.33* -0.57	-0.05 -0.16	-0.06 -0.19
Threshing percent	-0.05 -1.31	-0.03 0.06	0.04 0.12	0.05 -0.26
Plant height	-0.37** 0.45	0.43** 0.50	0.43** 0.22	0.32* 0.37
Panicle length	-0.02 -0.52	0.23 0.34	0.08 -0.03	-0.29* -0.69
Panicle girth	-0.28 -1.05	0.00 -0.05	-0.07 -0.14	0.00 -0.29
Stem girth	0.12 0.63	0.07 -0.27	-0.25 -1.42	0.20 0.54
Leaf width	0.20 -0.02	0.21 0.31	0.03 -0.15	0.05 -0.14
Panicles per plant	-0.13 0.41	-0.27 -0.63	-0.22 -0.87	0.00 -1.11

*, **Indicates significance at 0.05 and 0.01 levels, respectively.

correlations of GY with GI1 existed in C0 of the gene pools, but not in C1.

Phenotypically, GI1 was correlated ($P < 0.01$) in C0 and C1 of both gene pools only with PH. In Higrop C0 and C1, however, GI1 was positively correlated ($P < 0.01$) with BM and GI2, and negatively with HI. Bramel-Cox (1985) found GI1 was correlated only with BM (0.56). Genotypically, GI1 was negatively correlated with PG, PP, and HI in both gene pools. In C0 and C1 of Higrop, positive genotypic correlations existed for GI1 with BM and GI2, but in Senpop those correlations were weak. Negative genotypic correlations between GI1 and HI existed for both gene pools.

DISCUSSION

The beneficial effect of genes for high GI on other traits has been documented (Cox and Frey, 1984; Takeda and Frey, 1977; Bramel-Cox et al., 1986), although few reports exist about selection for increased GI. Increases in GI1 in Higrop and in Senpop were similar (Gupta et al., 1986) or lower (Takeda and Frey, 1987) than previously reported improvement of GI1 in oat. In the oat studies, only GI1 was selected and either all genetic variation for GI1 was exhausted (Gupta et al., 1986) or selected lines became tall and late (Takeda and Frey, 1987). In Higrop and Senpop, undesirable changes in unselected traits did not occur, likely because I culled lines which had excessively late BD or low GY. Similarly, Takeda and Frey (1987) reported that a 25% selection intensity for HI, followed by an 8% selection intensity for GI was the best selection protocol in oat for increasing both its GI and GY. Results from the oat studies and mine with pearl millet suggest that data for other agronomic traits should be considered when selecting for increased GI.

The formulas for estimating GI1 and GI2 use the same denominator (i.e., number of days to bloom + 10), so if vegetative dry weight remains constant after anthesis, as has been hypothesized (Bramel-Cox et al., 1984), then the two estimates of vegetative growth rate should be similar. Yet GI1 in Higrop and Senpop consistently was ca. 33% greater than GI2 (Table 2). This suggests that vegetative dry weight was not constant, seemingly because some of the vegetative matter had been

remobilized and translocated to grain. A more likely cause, however, was the presence of panicles in the vegetative dry weights used to estimate GI1, and their absence in the dry weights used to estimate GI2. Panicles occur in the dry weight samples used for GI1 because whole plants are harvested and dried at 10 days after bloom date, whereas the dry weight used for GI2 represents the plant parts remaining after panicles have been removed. The presence of panicles in the dry weight used for GI1 would cause it to be greater than GI2.

Perhaps of greater importance to future selection programs than the differences in magnitude of GI1 and GI2 is their correlation. If GI2 could be used instead of GI1, the cost of increasing vegetative growth rate would be reduced. Straw weights and BD are routinely measured in pearl millet trials, and therefore, GI2 could be estimated by a simple computation without sampling vegetative dry weight 10 days after BD. For Higrop, highly significant phenotypic correlations occurred between GI1 in both C0 and C1, and genotypic correlations were ca 0.90. Thus, future selection for vegetative growth rate in Higrop could be based upon GI2. However, in Senpop, phenotypic correlations between GI1 and GI2 were not significant, and genotypic correlations were low.

Inclusion of panicles in dry weight samples for GI1 implies that not only was vegetative growth rate selected, but also growth rate early in the reproductive phase of the plant. The contributions of the selection for panicle weight on the progress which occurred for BD, GY, and GI1 in Higrop and Senpop cannot directly be assessed from the data of my study.

However, because sample dry weights measured for GI2 included only vegetative portions of the plant, correlations of GI1 with GI2 provide information on the effect of panicles in samples for GI1 on the progress which occurred for BD, GY, and GI1. The high correlations between GI1 and GI2 in Higrop suggest that panicles in the dry weight samples of GI1 did not greatly impact the results from selection for GI1. The lack of correlation between GI1 and GI2 in Senpop suggests that panicles present in samples for GI1 had an effect on the progress that occurred for GY, BD, and GI1. A future study in which GI2 rather than GI1 was selected would provide more conclusive evidence on the effect of panicles in samples used to compute GI1 on gains from selection.

Bramel Cox et al. (1987) conducted a multivariate analysis to characterize associations among 17 traits, including GI1, measured on progenies derived from matings of adapted and exotic pearl millet parents. In their analysis, the first three principal components accounted for only 50% - 60% of the total variation. This indicated that associations among the traits were not strong, so selection of agronomically desirable segregates which possess high GI1 would be possible. The generally weak correlations among BD, GY, and GI1 and the changes in trait means that resulted from one cycle of selection in Higrop and Senpop support the conclusions of Bramel-Cox et al. (1987). Future selection of lines from Higrop and Senpop for high GI1 and GY and low BD should be successful, and few, if any, undesirable correlated changes are likely to occur in unselected agronomic traits.

Furthermore, grain yields and maturities in the C1 populations of Higrop and Senpop compare favorably with elite pearl millet varieties and hybrids (Lynch, 1993). Thus, Higrop and Senpop should be useful sources of future pearl millet varieties.

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GENERAL CONCLUSIONS AND DISCUSSION

Results from this dissertation research should be useful to plant breeders considering selection of vegetative growth index (GI) in pearl millet. The inheritance of GI measured 10 d after bloom date (GI1) and at maturity (GI2) and six traits related to GI, reported in Section I, indicated which breeding method will be most efficient for improving GI. The results from one cycle of recurrent selection in Higrop and Senpop, presented in Section II, showed that selection for increased GI1 was successful. The responses among unselected traits from selection for GI1, presented in Section III, showed that the changes that occurred among unselected traits were few.

Section I concluded that the inheritance of GI1, GI2, and traits related to GI in pearl millet are primarily controlled by additive and additive x additive epistatic genetic effects. A selection procedure which selects for these genetic effects should be effective for improving GI in pearl millet. However, because dominance genetic effects were important for GI2, maximum improvement when GI2 is selected, rather than GI1, will occur only if the selection method also selects for dominance genetic effects.

That means of other agronomic traits, such as grain yield or maturity, should be considered when selecting high GI1 progenies to form the next cycle of selection was shown in Section II. Selection was practiced in Higrop and Senpop for either (a) GI1 only, or (b) GI1, followed by culling of late maturing and/or low grain yielding lines.

When only GI1 was selected the improvement in GI1 in Higrop was 4.68% greater and in Senpop was 6.3% less than the improvement in GI1 when culling of high GI1 lines with late maturity and low grain yield was practiced. Additionally, the effects of culling on bloom dates and grain yields were positive: Bloom dates were 5.4% and 2.1% lower and grain yields 11.3% and 14.8% greater in Higrop and Senpop, respectively, than of C1 populations when culling was not practiced. Future cycles of selection should include culling of late maturity and/or low grain yielding lines. The largest correlated responses that resulted from selection for increased GI1 were increased panicle number per plant (13.6% and 14.3% of the C0 mean in Higrop and Senpop, respectively) and increased harvest index in Senpop (16.4% of the C0 mean) (Section III). In a multivariate analysis to characterize associations among 17 traits in germplasm similar to Higrop and Senpop, Bramel Cox et al. (1987) found no strong associations existed among the traits. Thus, selection of agronomically desirable high GI1 lines should be possible. The generally weak correlations among BD, GY, and GI1 and the favorable changes in means for BD, GY, and GI1 that resulted from one cycle of selection in Higrop and Senpop support their conclusions. Future cycles of selection in Higrop and Senpop for high GI1 should be successful, and few, if any, undesirable correlated changes are likely to occur in unselected agronomic traits.

Although selection increased grain yield in both gene pools, the underlying causes of the increases were different. In Higrop, growth

duration (i.e., bloom date) decreased 5%, but GI1 increased 7.1% and resulted in 3.0% greater biomass. The biomass increase in Higrop, combined with a slightly higher harvest index and threshing percent, resulted in more of biomass to occur as grain in Higrop C1 than occurred in Higrop C0. In Senpop, GI1 was increased 4.6%, but this was not enough to offset the shorter growth duration, resulting in a 5% decrease in biomass. However, harvest index in Senpop C1 was substantially increased (16% of the C0 mean), and this was sufficient to offset the 3.0% decrease in biomass, resulting in a 16.9% increase in grain yield in Senpop.

Bramel-Cox et al. (1984) hypothesized that GI1 and GI2 should estimate a common GI in pearl millet, and therefore should have similar values. That GI1 and GI2 were not measures of a common GI was shown a) by their different inheritance patterns (Section I), and b) by the consistently greater estimates of GI1 than GI2 (Section III). The different inheritance of GI1 and GI2 was attributed to a larger difference between the means for the F_1 s selfed and random mated that occurred for GI2 than occurred for GI1. The greater values of GI1 of Higrop and Senpop were attributed to the presence of panicles in dry weight samples for GI1, and their absence in GI2 dry weight samples. The relationship between the two estimates of GI in pearl millet is important because GI1 is more expensive to estimate than GI2. If equal gains could be obtained from selection for GI2, then future cycles of selection should be for GI2. At present however, the best information

available for deciding whether future selection should be for GI1 or GI2 are phenotypic and genotypic correlations between the two GI estimates. For Higrop, highly significant phenotypic correlations occurred between GI1 in both C0 and C1, and genotypic correlations were ca 0.90 (Section III). Thus, it appears that future selection for GI in Higrop could be based upon GI2. However, in Senpop, phenotypic correlations between GI1 and GI2 were not significant, and genotypic correlations were low. Initiating separate lines of descent in Higrop or Senpop and selecting for GI1 in one line of descent and GI2 in the other will provide the best information on whether selection of GI2 or GI1 is best.

Most pearl millet breeders do not possess the resources for conducting a sustainable recurrent selection program in two different gene pools for the same trait. In a choice between either Higrop or Senpop to undergo recurrent selection for GI1, Senpop should be chosen because: 1) Senpop C1 produced 55.1 g m² more grain and had a GI1 2.4 g m² d⁻¹ greater than did Higrop C0, despite equal bloom dates (53.3 d) in Senpop C1 and Higrop C0, and therefore equal growth durations (Fussel and Pearson, 1978); 2) After only one cycle of selection, Senpop C1 had 12% greater GY and 17% greater GI1 than ICMV 82132, the parent variety used to form Higrop and Senpop with highest GY and GI1, whereas Higrop C1 had 10% lower GY and only 2% greater GI1 than ICMV 82132; and 3) The direction, magnitude, and percent of change from C0 to C1 were more favorable in Senpop than Higrop, and genotypic variances in the C1 of Senpop generally were greater than in the C1 of Higrop.

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APPENDIX

Table A1. Abbreviations of traits presented in Appendix tables and their units of measure.

Abbreviation	Trait	Units
PY	Panicle yield	g m^{-2}
GY	Grain yield	g m^{-2}
SY	Straw yield	g m^{-2}
BD	Bloom date	d after sowing
BM	Biomass	g m^{-2}
GI1	Growth index 1	$\text{g m}^{-2} \text{ d}^{-1}$
GI2	Growth index 2	$\text{g m}^{-2} \text{ d}^{-1}$
HI	Harvest index	%
TP	Threshing percent	%
PH	Plant height	cm
PL	Panicle length	cm
PG	Panicle girth	mm
SG	Stem girth	mm
LW	Leaf width	mm
PP	Panicles per plant	# plant ⁻¹

Table A2. Means for bloom date of parent populations per-se and self pollinated and F_1 s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	das				
3226	46 (47)	47 46 46	51 53 51	46 46 47	47 46 46
3175		49 (48)	52 49 51	47 45 46	48 47 48
6098			65 (60)	53 50 50	52 58 60
ECC6				45 (48)	40 45 50
VCF2					50 (51)

Table A3. Means for GII of parent populations per-se and self pollinated and F_1 s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	$g\ m^{-2}\ d^{-1}$				
3226	5.37 (5.28)	4.28 5.53 3.78	5.63 6.11 5.90	5.88 5.28 4.97	5.27 4.93 4.18
3175		4.10 (4.20)	5.78 6.13 5.38	5.23 4.70 4.60	5.68 4.97 4.65
6098			na (5.53)	6.23 5.43 7.01	6.78 7.13 7.28
ECC6				4.90 (4.93)	7.48 5.21 4.23
VCF2					5.07 (5.33)

Table A4. Means for GI2 of parent populations per-se and self pollinated and F_1 s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	$g\ m^{-2}\ d^{-1}$				
3226	4.67 (5.31)	4.37 4.15 3.87	6.82 6.98 5.80	5.93 5.60 3.58	6.43 5.71 4.18
3175		4.95 (4.97)	6.38 7.08 5.28	5.77 5.65 4.93	6.32 6.05 3.82
6098			4.03 (5.23)	5.52 4.62 4.25	7.30 5.45 5.45
ECC6				4.71 (4.20)	9.07 5.13 3.87
VCF2					3.71 (3.50)

Table A5. Means for straw yield of parent populations per-se and self pollinated and F₁s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	g m ⁻²				
3226	261	247	415	326	361
	(297)	225	430	312	317
		213	355	204	234
3175		285	393	326	362
		(284)	410	307	342
			320	276	219
6098			304	345	451
			(362)	275	395
				250	383
ECC6				254	341
				(241)	281
					230
VCF2					221
					(211)

Table A6. Means for biomass of parent populations per-se and self pollinated and F₁s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	$g\ m^{-2}$				
3226	538	466	764	728	739
	(531)	435	745	640	677
		356	616	406	476
3175		482	701	627	670
		(443)	743	657	659
			550	507	438
6098			525	682	898
			(625)	592	767
				558	668
ECC6				558	668
				(516)	650
					479
VCF2					500
					(441)

Table A7. Means for harvest index of parent populations per-se and self pollinated and F_1 s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
			%		
3226	35	31	31	39	35
	(28)	32	26	37	38
		24	29	34	34
3175		25	38	35	31
		(22)	31	34	34
			27	29	35
6098			24	34	37
			(27)	38	35
				39	31
ECC6				39	43
				(38)	43
					40
VCF2					43
					(38)

Table A8. Means for plant height of parent populations per-se and self pollinated and F_1 s per-se, self pollinated, and random mated from generation means analysis.

Parent name	Parent Name				
	3226	3175	6098	ECC6	VCF2
	cm				
3226	154	138	173	153	173
	(148)	138	184	155	156
		138	173	142	139
3175		144	183	148	163
		(148)	173	147	153
			167	141	141
6098			225	178	196
			(196)	167	203
				173	194
ECC6				147	171
				(153)	158
					153
VCF2					165
					(163)

Table A9. Analysis of variance for several traits of pearl millet in 1990 and 1991 in two years at ICRISAT Center for generation means study.

Source of variation	df	Traits						
		BD	GI1	GI2	SY	BM	HI	PH
Years	1	731.5**	445.9**	302.4**	701599.1**	2871466.3**	569.5**	153458.0**
Reps/Years	4	3.8	27.9**	16.1**	73725.4**	351602.7**	1.5	679.9**
Entry	48	126.4**	5.3*	8.0**	27120.5**	93603.6**	255.4**	2690.4**
Checks	8	109.7**	7.6**	5.5**	28803.3**	73969.8**	80.4**	3930.0**
Checks vs. Generations	1	10.7	4.2	4.5*	11269.6	235628.9**	4646.9**	791.1**
Generations	39	132.8**	4.9**	8.6**	27181.8**	93989.3**	178.9**	2484.9**
Entry x Years	48	16.5	2.8	3.9	9107.6*	23806.0	14.1	206.6
Checks x Years	8	8.3	4.7	2.7	7246.8	33787.1	18.9	147.5
Generations x Years	39	18.5	2.1	4.2	9672.4**	22601.5	13.5	213.7
Error	190	10.6	2.8	2.5	4730.5	15050.0	13.7	205.3

*, **Indicates significance at 0.05 and 0.01 levels, respectively.

Table A10. Mean squares, means, and coefficients of variation for S₁ lines of Higrop C₀ and C₁ evaluated at two locations in 1991.

Source	df	PY ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Loc	1	121942**	38631**	3780**	22687619**	8002**	4657**	2671.2**
Loc(Rep)	3	16896*	4508	143**	1133628**	40*	234**	28.7**
Cycle (C)	1	56405	36827*	890	92368	98	35	15.0
Loc x C	1	44849*	13150	414*	12031	104*	5	14.9*
Lines(C)	90	10285	7174*	107*	150124*	23	19*	8.5*
C0	45	12612	8012*	80*	164929*	24	22*	8.8*
C1	45	9524	6337	134*	134489*	25	16*	8.0*
Loc x Lines(C)	90	8733*	4858	28*	85317	17*	10	4.0*
Error	273	6349	3708	8	84607	12	11	2.2
Mean		287	203	57.6	893	13.2	8.8	25.3
CV		27	29	5	32	25	37	18

^aerror df=263

^berror df=250

^cactual value = 1×10^{-3}

*,** indicates significance at 0.05 and 0.01 levels, respectively.

Table A10. (Continued)

Source	df	TP ^{ac}	PH	PL	PG	SG	LW	PP
Loc	1	27.8**	961520**	592**	1121**	1574**	18393**	247**
Loc(Rep)	3	16.5*	1223**	7	24	12**	66	5**
Cycle (C)	1	9.3	488	478**	20	7	160	10
Loc x C	1	6.1	11	68	18	6	23	10**
Lines(C)	90	11.0*	1141*	34*	28*	2	77*	1*
C0	45	16.1*	933*	41*	35*	3	55*	1*
C1	45	10.9*	1349*	28*	22*	2	100*	1*
Loc x Lines(C)	90	4.3	501*	8*	13	2	31	1*
Error	273	5.2	286	4	11	2	27	0.4
Mean		70.4	207	22	27	11	38	2.4
CV		10	8	9	12	12	14	27

Table A11. Mean squares, means, and coefficients of variation for S₁ lines of Senpop C₀ and C₁ evaluated at two locations in 1991.

Source	df	PY ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Loc	1	262231**	96675**	7053**	28303110**	7818**	5512**	3377**
Loc(Rep)	3	31225**	13382**	92**	2014326**	46*	305**	14.4**
Cycle (C)	1	204902	116369	2635	23797	43	14	166.2
Loc x C	1	270648**	156713**	953**	818	53**	0.4	99.9**
Lines(C)	90	19303**	11964**	110**	258295	23*	38	12.4**
C0	45	22985**	13645**	120**	332392	26**	36	12.4**
C1	45	15567	10282**	99**	185025	20*	41*	12.5**
Loc x Lines(C)	90	11117*	6736*	32*	1220340*	17	22	4.2*
Error	273	6863	4098	9	162359	14	28	2.2
Mean		286	205	59.8	928	13.3	9.0	25.1
CV		29	31	5	43	27	59	18

^aerror df=266

^berror df=251

^cactual value = 1×10^{-3}

*, ** indicates significance at 0.05 and 0.01 levels, respectively.

Table A11. (Continued)

Source	df	TP ^{ac}	PH	PL	PG	SG	LW	PP
Loc	1	20.3**	973578**	487**	1319**	1765**	17891**	278**
Loc(Rep)	3	4.7	1830**	62**	3	17**	27	13**
Cycle (C)	1	10.2	12098**	279*	324*	16	67	13**
Loc x C	1	11.9**	43	13	59*	5	33	0.6
Lines(C)	90	8.9*	1061**	33**	25**	3*	66**	1.2
C0	45	10.2**	1240**	44**	25**	3*	67**	1.1
C1	45	9.1*	883**	23**	25**	3*	66**	1.3
Loc x Lines(C)	90	6.2*	489*	10*	12*	2*	27	1.3*
Error	273	4.5	251	4	7	1.4	22	0.7
Mean		70.9	206	23	27	11	39	2.2
CV		9	8	9	10	11	12	39

Table A12. Mean squares, means, and coefficients of variation for S_1 lines of Higrop C_0 and C_1 evaluated at Hisar in 1991.

Source	df	Py ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Rep	2	15525	2440	143**	1668690**	49.0	350.6**	40.3**
Cycle (C)	1	101063**	48917*	1296**	92896	200.8*	36.1	29.1
Line (C)	90	11132*	7354**	116**	199205**	32.0**	26.4**	8.4**
	C0 45	11977*	7766*	86**	224885**	35.8**	29.9**	8.3**
	C1 45	10287	6943*	145**	173524**	28.8**	2.9	8.4**
Error	182	7467	4446	10	14970	14.2	15.0	2.5
Mean		274	195	59.9	1075	16.6	11.4	19.1
CV		31	33	5	32	22	34	26

^aerror df=174

^berror df=170

^cactual value = 1×10^{-3}

*, ** indicates significance at 0.05 and 0.01 levels, respectively.

Table A12. (Continued)

Source	df	TP ^{ac}	PH	PL	PG	SG	LW	PP
Rep	2	11.3	1809.5**	6.5	21.6	17.6**	38.2	0.67
Cycle (C)	1	2.2	224.6	137.8*	0.5	12.6*	35.4	0.21
Line (C)	90	13.0	1160.5**	25.7**	18.4**	2.9**	65.7**	0.63**
C0	45	13.1	973.4**	32.3**	20.1**	3.6**	49.7*	0.59**
C1	45	12.8	272.4	19.1**	16.7**	2.2**	81.7**	0.66**
Error	182	12.3	272.4	3.2	8.9	1.1	30.0	0.31
Mean		71.7	244	22	28	12	43	1.8
CV		15	7	8	11	9	13	31

Table A13. Mean squares, means, and coefficients of variation for S_1 lines of Senpop C_0 and C_1 evaluated at Hisar in 1991.

Source	df	PY ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Rep	2	42054*	15012	89**	3011088**	68.0*	456.9**	19.0**
Cycle (C)	1	467405**	264822**	3515**	150401	91.8	10.5	265.6**
Line (C)	90	20483**	12662**	117**	339017*	29.6**	56.1	10.9**
C0	45	24915**	14550**	124**	413502*	36.1**	50.1	12.4**
C1	45	16051**	10774**	110**	264531	25.1*	64.0	9.5**
Error	182	6948	4198	11	232148	16.2	41.6	2.1
Mean		266	193	63.0	1130	16.6	11.8	18.1
CV		31	33	5	42	23	55	25

^aerror df=177

^berror df=170

^cactual value = 1×10^{-3}

*, ** indicates significance at 0.05 and 0.01 levels, respectively.

Table A13. (Continued)

Source	df	Tp ^{ac}	PH	PL	PG	SG	LW	PP
Rep	2	7.3	2743.8**	19.3*	1.0	20.7**	26.4	0.17
Cycle (C)	1	13.1	7979.2**	123.1**	352.7**	19.8**	7.3	10.94**
Line (C)	90	10.7**	1170.9**	24.4**	18.4**	2.4**	45.9*	0.68**
C0	45	13.1**	1366.3**	31.8**	20.7**	2.8**	46.9**	0.79**
C1	45	8.4	975.6**	16.8**	16.0**	1.9	44.9**	0.57**
Error	182	5.9	291.1	3.5	7.4	1.3	20.5	0.26
Mean		71.4	244	24	28	13	44	1.6
CV		10	7	8	10	9	10	32

Table A14. Mean squares, means, and coefficients of variation for S_1 lines of Higrop C_0 and C_1 evaluated at ICRISAT Center in 1991.

Source	df	PY ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Rep	1	13487	8645	143**	11886	20.6	1.3	4.3
Cycle (C)	1	191	1059	9.6	11503	1.0	4.0	0.3
Line (C)	90	8024**	4678**	19.6**	35184**	8.1*	3.1*	4.1**
C0	45	3688	5157**	4.6	43130**	8.5*	3.7**	5.5**
C1	45	6338*	4198**	21.0**	27666	7.8	2.3	3.6**
Error	91	44435	2316	4.8	20024	5.7	2.0	1.9
Mean		307	214	54.1	621	8.0	4.9	34.7
CV		21	22	4	22	27	28	12

^aerror df=87

^berror df=77

^cactual value = 1×10^{-3}

*,** indicates significance at 0.05 and 0.01 levels, respectively.

Table A14. (Continued)

Source	df	Tp ^{ac}	PH	PL	PG	SG	LW	PP
Rep	1	1.4	49.0	7.8	29.0	0.09	120.6*	14.9
Cycle (C)	1	14.8*	275.1	408.0**	37.4	0.09	137.4	19.1**
Line (C)	90	4.1**	481.6**	16.3**	23.1**	1.95	42.5**	1.1
C0	45	18.4**	420.6*	17.6**	31.8**	1.5	42.7**	0.6
C1	45	4.8**	542.7**	15.1**	14.3	2.4	42.3**	1.4
Error	91	1.9	249.6	5.7	13.9	2.6	22.5	0.8
Mean		69.4	151	20	25	9	30	3.3
CV		6	11	12	15	18	16	23

Table A15. Mean squares, means, and coefficients of variation for S_1 lines of Senpop C_0 and C_1 evaluated at ICRISAT Center in 1991.

Source	df	PY ^a	GY ^a	BD	BM ^a	GI1 ^b	GI2	HI ^{ac}
Rep	1	10661	10121	97.6**	17952	0.8	0.2	5.2
Cycle (C)	1	13616	8261	73.1	80086	4.2	3.4	0.1
Line (C)	90	10094*	6037*	24.7**	40031**	9.0	3.2**	5.7**
C0	45	12372*	7173*	29.9**	53239**	11.0	4.0**	4.9**
C1	45	7703	4902	19.5**	26588	7.1	2.3	6.4**
Error	91	6681	3899	5.0	23278	8.7	1.7	2.4
Mean		315	222	55.0	624	8.2	4.7	35.6
CV		26	27	4	24	34	28	14

^aerror df=89

^berror df=81

^cactual value = 1×10^{-3}

*,** indicates significance at 0.05 and 0.01 levels, respectively.

Table A15. (Continued)

Source	df	TP ^{ac}	PH	PL	PG	SG	LW	PP
Rep	1	8.2	1.2	146.2**	6.3	9.1**	29.0	38.6**
Cycle (C)	1	4.2	4161.0**	168.3**	29.8	0.7	93.3	2.9
Line (C)	90	5.5*	379.4*	18.1**	18.5**	2.8**	46.9**	1.8
C0	45	5.5	476.1**	22.2**	14.9**	2.7**	42.5*	1.7
C1	45	6.3*	282.8*	14.0**	22.2**	2.8**	51.2**	1.9
Error	91	3.8	171.6	5.8	1.6	1.3	24.3	1.7
Mean		70.0	150.1	22	25	9	32	3.1
CV		9	9	11	10	15	16	41

Table A16. Mean squares, means, and coefficients of variation for cycle-populations evaluated at three locations in 1991.

Source	df	PY	GY	BD	BM	GI1 ^a	GI2 ^b	HI ^c
Loc	2	754055**	516123**	8240**	11600727**	15561**	4570**	2586.6**
Rep(Loc)	9	79397**	52878**	74**	590010**	136**	86**	9.3**
Entry (C)	48	25244	16022	125**	199730*	41**	34**	15.6**
Entry x Location	96	18608**	11552**	16**	117731	16**	18*	4.3**
Error	422	10233	5973	5	93631	11	14	1.8
Mean		320	227	51.3	884	15.6	9.4	27.6
CV		31	34	4	34	21	39	15

^aerror df=394

^berror df=407

^cactual value = 1×10^{-3}

*, ** indicates significance at 0.05 and 0.01 levels, respectively.

Table A16. (Continued)

Source	df	TP ^c	PH	PL	PG	SG	LW	PP
Loc	2	199.5**	620165**	681**	859**	506**	9636**	292**
Rep(Loc)	9	37.6**	8190**	21**	11*	11**	157**	2*
Entry (C)	48	3.1	3773**	65**	64**	7**	216**	10**
Entry x Location	96	5.3	766*	11*	10**	2**	32*	1
Error	422	4.2	315	8	5	1	24	1
Mean		69.7	213	24	26	10	39	2.8
CV		9	8	12	9	11	13	33

Table A17. Mean squares, means, and coefficients of variation for cycle-populations evaluated at ICRISAT Center in 1991.

Source	df	PY	GY	BD	BM	GI1 ^a	GI2 ^a	HI ^b
Rep	3	149996**	95475**	31**	697047**	82**	49**	4.6**
Entry	48	28117**	18029**	32**	84227	9**	5	6.5**
Error	136	16491	9470	5	60097	5	5	1.2
Mean		362	262	51.5	644	7.1	4.6	40.7
CV		34	36	4	37	27	43	9

^aerror df=125

^bactual value = 1×10^{-3}

** indicates significance at 0.01 level.

Table A17. (Continued)

Source	df	Tp ^b	PH	PL	PG	SG	LW	PP
Rep	3	8.3**	2426**	12	10.4	1.2	225**	2.3
Entry	48	4.7**	946**	32**	29.9**	1.9**	105**	5.6**
Error	136	2.0	154	5	7.7	1.1	15	1.0
Mean		71.6	148	22	24	8.8	30.6	4.1
CV		6	9	10	11	12	12	23

Table A18. Mean squares, means, and coefficients of variation for cycle-populations evaluated at Bhavanisagar in 1991.

Source	df	PY	GY	BD	BM	GI1 ^a	GI2	HI ^b
Rep	3	3269	1394	2	11190	7	3	1.2
Entry	48	14149**	10136**	21**	127561**	49**	25**	7.1**
Error	144	5714	3540	1	46352	15	9	1.2
Mean		349	251	44.8	1131	24.9	14.2	22.5
CV		22	24	2	19	15	21	15

^aerror df=138

^bactual value = 1×10^{-3}

** indicates significance at 0.01 level.

Table A18. (Continued)

Source	df	TP ^b	PH	PL	PG	SG	LW	PP
Rep	3	0.1	373**	6	7.2	28.8**	22.7	2.4
Entry	48	4.2**	2604**	32**	43.2**	6.7**	118.6**	4.6**
Error	144	2.7	14	5	3.8	1.5	19.6	1.0
Mean		71.5	248	26	26	10	44	2.3
CV		7	6	9	8	13	10	43

Table A19. Mean squares, means and coefficients of variation for cycle-populations evaluated at Hisar in 1991.

Source	df	PY	GY	BD	BM	GI1 ^a	GI2	HI ^b
Rep	3	84927**	61764**	190**	1061793**	319**	207**	22.2**
Entry	48	20194**	10959**	103**	223404	16	39	11.3**
Error	144	8698	5029	10	168283	14	28	2.9
Mean		249	168	57.7	877	15.0	9.3	19.5
CV		37	42	6	47	25	57	27

^aerror df=131

^bactual value = 1×10^{-3}

*, ** indicates significance at 0.05 and 0.01 levels, respectively.

Table A19. (Continued)

Source	df	TP ^b	PH	PL	PG	SG	LW	PP
Rep	3	104.2**	21772**	45.3**	16.6**	1.6	222.9**	0.9
Entry	48	8.6	1756**	22.9*	11.0**	2.4**	56.8*	2.8**
Error	144	8.1	575	14.7	2.2	0.8	38.8	0.8
Mean		66.0	243	24	28	12	41	1.9
CV		14	10	16	8	8	15	43

Table A20. Phenotypic (above diagonal) and genotypic (below diagonal) correlations among several traits computed from S₁ lines of C₁ of the Higrop gene pool grown at two locations in 1991.

	BD	PY	GY	BM	GI1	GI2	HI	TP	PH	PL	PG	SG	LW	PP
BD	1.00 ^a	0.02	1548	0.60	0.29	0.38	-0.45	0.41	0.70	0.49	-0.37	0.52	0.09	-0.16
PY	0.20	1.00	0.90	0.53	0.33	0.37	0.32	0.01	0.07	0.02	0.10	0.02	0.17	0.01
GY	0.42	0.70	1.00	0.53	0.30	0.35	0.44	0.41	0.17	0.10	0.04	0.13	0.27	-0.14
BM	0.78	0.61	0.63	1.00	0.59	0.93	-0.44	0.21	0.58	0.24	-0.27	0.31	0.22	-0.01
GI1	0.42	0.23	0.20	0.78	1.00	0.57	-0.33	-0.03	0.43	0.23	0.00	0.07	0.21	-0.27
GI2	0.58	0.49	0.49	0.94	0.86	1.00	-0.53	0.10	0.49	0.09	-0.22	0.21	0.23	0.06
HI	-0.60	0.10	0.27	-0.63	-0.57	-0.66	1.00	0.27	-0.46	-0.11	0.32	-0.18	0.05	0.16
TP	-0.52	-0.61	0.24	0.11	0.06	0.10	0.00	1.00	0.37	0.19	-0.21	0.26	0.20	-0.29
PH	0.90	0.02	0.23	0.71	0.50	0.56	-0.76	0.46	1.00	0.48	-0.24	0.26	0.19	-0.19
PL	0.68	-0.04	0.26	0.47	0.34	0.27	-0.17	0.56	0.65	1.00	-0.11	0.21	0.04	-0.19
PG	-0.53	0.19	0.03	-0.48	-0.05	-0.45	0.51	-0.49	-0.56	-0.22	1.00	-0.10	0.30	-0.33
SG	1.25	0.83	1.63	0.43	-0.27	-0.18	0.50	1.56	0.56	0.53	-0.72	1.00	0.30	-0.30
LW	0.18	0.37	0.67	0.25	0.31	0.21	0.16	0.61	0.19	0.01	0.32	0.38	1.00	-0.25
PP	-0.22	-0.32	-0.74	-0.07	-0.63	0.17	-0.45	-0.68	-0.20	-0.30	-0.62	-0.95	-0.95	1.00

^aCoefficients greater than ± 0.12 or ± 0.16 are significant at 0.05 or 0.01 level, respectively.

Table A21. Phenotypic (above diagonal) and genotypic (below diagonal) correlations among several traits computed from S_1 lines of C_1 of the Senpop gene pool grown at two locations in 1991.

	BD	PY	GY	BM	GI1	GI2	HI	TP	PH	PL	PG	SG	LW	PP	
BD	1.00 ^a	-0.24	-0.27	0.14	-0.01	-0.05	-0.56	-0.22	0.40	-0.19	0.31	0.50	0.36	-0.26	
PY	-0.01	1.00	0.96	0.32	0.15	0.09	0.66	0.29	0.01	0.16	0.13	0.06	-0.07	0.31	
GY	-0.10	0.98	1.00	0.37	0.14	0.16	0.69	0.52	0.07	0.13	0.08	0.03	-0.07	0.34	
BM	0.42	0.21	0.25	1.00	0.22	0.94	-0.22	0.28	0.57	-0.29	0.13	0.21	0.10	0.20	
GI1	0.11	-0.07	-0.17	0.15	1.00	0.17	-0.06	0.05	0.32	-0.29	0.00	0.20	0.05	0.00	
GI2	0.14	-0.15	-0.05	0.89	0.08	1.00	-0.27	0.27	0.49	-0.31	0.00	0.08	0.06	0.19	
HI	-0.65	0.71	0.74	-0.35	-0.19	-0.38	1.00	0.43	-0.40	0.26	-0.22	-0.27	-0.14	0.31	
TP	-0.40	0.37	0.55	0.32	-0.26	0.40	0.47	1.00	0.21	-0.05	-0.17	-0.09	-0.11	0.19	
PH	0.52	-0.13	-0.07	0.67	0.37	0.61	0.61	-0.47	1.00	-0.17	0.17	0.40	0.31	0.06	
PL	-0.11	-0.10	-0.13	-0.61	-0.69	-0.64	0.19	-0.21	-0.27	1.00	-0.09	-0.06	0.09	0.00	
PG	0.58	0.01	-0.09	0.11	-0.29	-0.15	-0.40	-0.47	0.01	-0.28	1.00	0.61	0.27	-0.38	
SG	0.90	0.12	-0.09	-0.01	0.54	-0.39	-0.51	-0.77	0.58	-0.02	1.30	1.00	0.43	-0.30	
LW	0.75	-0.47	-0.51	0.17	-0.14	0.10	-0.45	-0.60	0.46	-0.09	0.25	1.11	1.00	-0.04	
PP	-0.74	0.85	1.08	1.42	-1.11	1.52	0.80	1.02	1.37	-0.21	-1.69	-2.43	-0.40	1.00	

^aCoefficients greater than ± 0.12 or ± 0.16 are significant at 0.05 or 0.01 level, respectively.